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FOSSIL SMALL MAMMALS FROM THE HARRISON FORMATION (LATE ARIKAREEAN: EARLIEST MIOCENE), CHERRY COUNTY, NEBRASKA

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Abstract

Microvertebrate fossils from the easternmost known exposure of the Harrison Formation in Cherry County, Nebraska, represent at least 29 mammalian species, constituting the McCann Canyon local fauna. Twenty species are rodents or lagomorphs. Three new genera and six new species of rodents and two new species of insectivores are described. The age of the fauna is early late Arikareean (earliest Miocene), which compares closely to the age of faunas described from the Monroe Creek Formation of South Dakota. The McCann Canyon local fauna includes the earliest occurrence of the talpids *Mystipterus* and *Scalopoides* and the latest occurrence of the insectivores *Domnina, Centetodon,* and the yoderimyine rodents. The presence of the typically European rodents *Parallomys* and *Pseudotheridomys* in the McCann Canyon fauna provides a link with Hemingfordian faunas. The McCann Canyon local fauna is intermediate in age between faunas of early Arikareean and early Hemingfordian age.

Introduction

Tedford et al. (1987) recognized the late Arikareean based on the faunas from the Harrison and Upper Harrison (=Marsland) formations of Nebraska. This interval is recognized mainly on the basis of the large mammal fauna from the Agate Springs fossil beds, Sioux County, Nebraska, which is in the Upper Harrison Formation. It represents the very latest fauna of the late Arikareean age. The primarily large mammal fauna from the older and subjacent Harrison Formation has never been reviewed. The only rodents described from either the Harrison or Upper Harrison are palaeocastorine beavers (L. D. Martin, 1987) and the geomyoid rodents *Gregorymys, Proheteromys* and *Dikkomys* (Wood, 1936*b*), the latter two known only from isolated teeth collected from anthills.

The McCann Canyon local fauna is significant because of its stratigraphic and biostratigraphic occurrence, and its abundance of micromammals. The fossils described here from Cherry County represent a geographically distinct fauna of early late Arikareean age, which permits biostratigraphic correlation with other Arikareean faunas from the Rocky Mountain region (McKenna and Love, 1972; Nichols, 1976; Rensberger, 1981), the John Day Formation of Oregon (Rensberger, 1971, 1973), and those of early Arikareean age described from the Great Plains (J. R Macdonald, 1963, 1970; L. J. Macdonald, 1972).

The only comprehensive study of a micromammalian fauna from the Arikareean of Nebraska was that of L. D. Martin (1973), who studied the fauna from the early Arikareean Gering Formation of Dawes, Scottsbluff, and Morrill counties, Nebraska. Some parts of his work have been published (L. D. Martin, 1974, 1980), but most of the Arikareean microfauna from Nebraska is undescribed. The

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large sample of micromammals described here is from strata referred to the Harrison Formation, Cherry County, Nebraska, and represents a younger fauna than that described by Martin. It is also considerably farther east than Martin's study area.

Abbreviations for institutions cited below are: AMNH, American Museum of Natural History; FAM, Frick Collections, American Museum; FMNH, Field Museum of Natural History; LACM, Museum of Natural History, Los Angeles County; SDSM, South Dakota School of Mines and Technology, Museum of Geology; SMNH, Saskatchewan Museum of Natural History; UC, University of Chicago; UNSM, University of Nebraska State Museum; UW, University of Wyoming, Museum of Geology.

HISTORY OF INVESTIGATION

The "Mouth of McCann Canyon Quarry" (UNSM locality Cr-117) was first identified by Skinner et al. (1977) as the easternmost occurrence of the Harrison Formation in Nebraska (Fig. 1). They mentioned but did not describe a colubrid snake and a beaver, *Palaeocastor fossor,* from this quarry. Later, the identification of the beaver was changed to *Euhapsis barbouri* (Skinner and Johnson, 1984), and as many as 17 additional mammalian species were cited as being represented, but were not listed. Holman (1981) described the herpetofauna of this locality on the basis of collections made by R. Evander of the UNSM from 1978 to 1980. From 1981 to 1986, collection of microvertebrates at UNSM Cr-117 was carried out principally by the University of Nebraska State Museum. In the summer of 1986 a second fossiliferous quarry of identical lithology and apparent stratigraphic position was discovered. This second quarry, UNSM Cr-125, is approximately 1.2 km (0.75 miles) east of Cr-117 (NW ¼, sec. 33, T33N, R31W), in a roadcut on the north bank of the Niobrara River. Skinner and Johnson (1984:fig. 32, section 25) measured a section at this site, their Olson Ranch locality, but collected no fossils from it. It has produced a fauna identical to that of Cr-117. Cr-125 may be an eastern extension of the fossiliferous bed present at Cr-117, but exact correlation cannot be determined due to present topography and groundcover. Most of the fossil material from Cr-125 was collected from 1986 to 1988 by B. Bailey of the State of Nebraska Department of Roads as part of the Highway Salvage Paleontology Program.

GEOLOGY

The sediments referred to the Harrison Formation in Cherry County, Nebraska, were described by Skinner et al. (1977:290–292) as ". . . windblown, and consists mostly of consolidated massive beds of silt and fine 'pepper and salt' sand with an overall gray appearance." In its type area in Sioux County, Nebraska, the Harrison Formation has a thickness up to 61.5 m (=200 ft; see Hatcher, 1902). At its easternmost extension along the Niobrara River in Cherry County, the Harrison Formation is only 4.3 m (14 ft) thick in surface exposures (Skinner and Johnson, 1984) and unconformably overlies a ". . . buff siltstone referable to the Rosebud Formation or to a Monroe Creek equivalent" (Skinner and Johnson, 1984:233) and is unconformably overlain by the Crookston Bridge Member of the Valentine Formation.

The beds referred to the Harrison Formation at Cr-117 and Cr-125 are not laterally continuous with the formation in its type area but have the distinctive lithology of the Harrison Formation ("salt and pepper" appearance, silty to fine

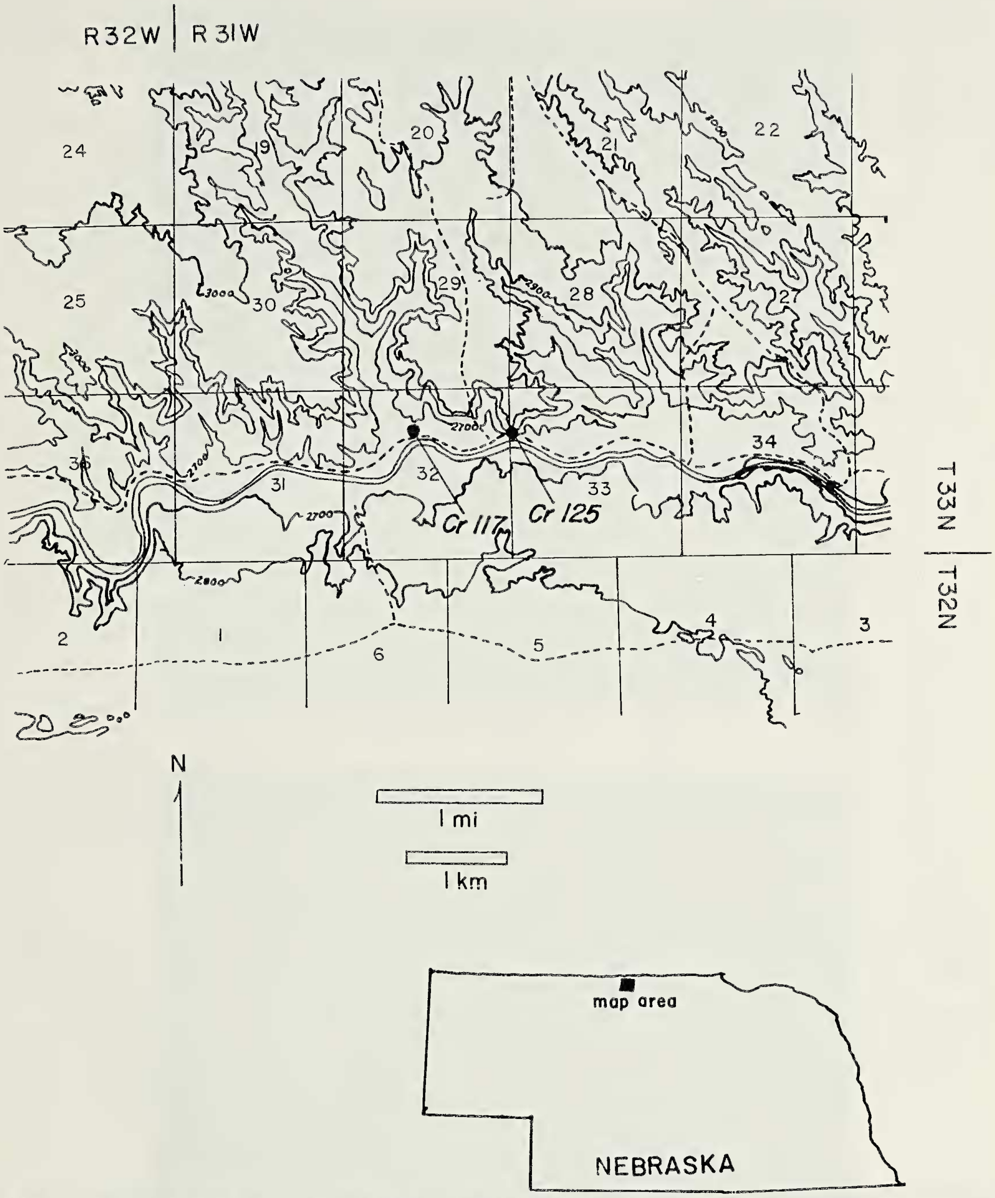

Fig. 1.—Map showing location of UNSM localities Cr-117 and Cr-125, Cherry County, Nebraska.

sand-sized texture of eolian origin, and randomly occurring channel sands containing clastic pebbles of fine sandstone or siltstone; Skinner et al., 1977).

The fossils from Cr-117 are derived from two thin beds or lenses (5 to 10 cm thick) of poorly sorted channel sand containing sandstone pebbles (Fig. 2A), less than 0.5 to 1 m above the roadbed. Since the original description of the fossiliferous layers at Cr-117, a narrow, deep gully has been cut along the west end of the roadcut. In this new exposure, the two fossiliferous lenses can be seen to merge toward the north, forming a layer about 1 m (3 ft) thick. At Cr-125, the fossiliferous

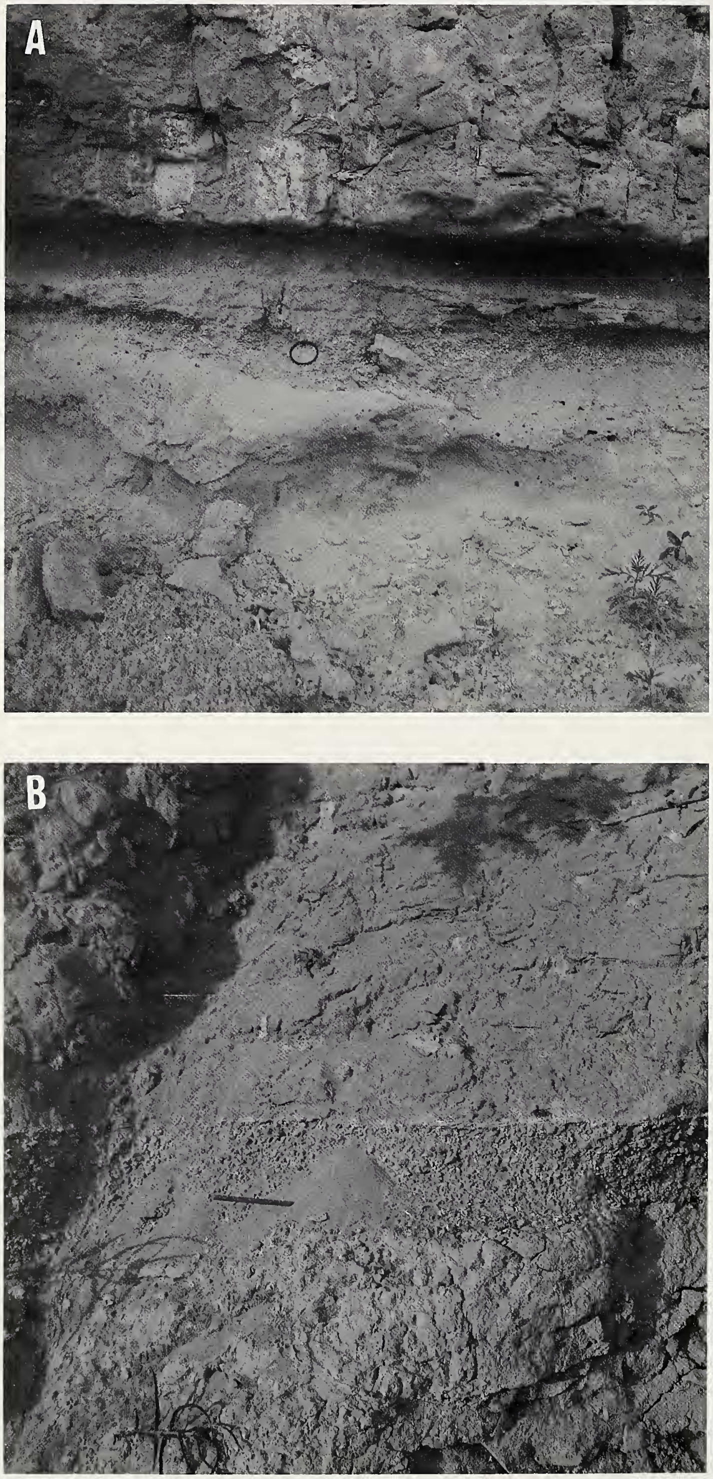
A
B

Table 1.—*Occurrence of mammalian taxa in the McCann Canyon local fauna compared with other micromammalian faunas of the Great Plains. S/G = Sharps fauna, South Dakota and Gering fauna, Nebraska; MC = Monroe Creek fauna, South Dakota.*

	Cr-117	Cr-125	S/G	MC
Herpetotherium youngi	X	X	X	X
Centetodon divaricatus	X			
Parvericius voorhiesi	X	X		
Amphechinus sp.		X		
Ocajila sp.		X		
Scalopoides sp.	X			
Proscalops secundus	X	X		
Mystipterus sp.		X		
Domnina sp.		X		
Alwoodia harkseni	X	X		X
Parallomys americanus	X	X		X
Promylagaulus riggsi	X	X		
Trilaccogaulus ovatus	X	X		X
Nototamias quadratus	X	X	X	X
Protosciurus sp.		X		
Palaeocastor cf. *P. simplicidens*	X	X		X
Proheteromys sp.	X	X		
Hitonkala macdonaldtau	X	X		
Sanctimus cf. *S. stuartae*	X	X	X	
Florentiamys sp.	X			
Entoptychus grandiplanus	X	X		
Gregorymys cf. *G. formosus*	X			X
Arikareeomys skinneri	X	X		
Pseudotheridomys sp.	X	X		X
Leidymys cerasus	X	X		
Paciculus nebraskensis	X	X		
Plesiosminthus cf. *P. clivosus*	X			X
Gripholagomys lavocati	X	X		
Archaeolagus cf. *A. primigenius*	X	X		X

layer is identical in lithology to those at Cr-117, is approximately 1.5 m (5 ft) above the roadbed, and ranges from 20 to 50 cm in thickness (Fig. 2B). While the Harrison Formation is almost entirely eolian in origin (Skinner et al., 1977), the beds that contain the fossil material are clearly fluvial conglomerates contained within the otherwise eolian stratum. These beds contain some cross-bedding as well as clasts of sandstone apparently derived directly from the surrounding Harrison Formation. The fossils show moderate water wear.

FAUNA

Nearly all of the species from the McCann Canyon local fauna are represented from both fossil localities (Table 1). The differences between the faunas from the two localities are most likely due to sampling error as the species not common to both localities are each known from fewer than three specimens.

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Fig. 2.—Fossiliferous conglomeratic layers in the Harrison Formation, Cherry County, Nebraska. A, UNSM locality Cr-117, Mouth of McCann's Canyon (lens cap in center 5 cm in diameter). B, UNSM locality Cr-125, Olson Ranch (probe handle, left of center, 10 cm in length). Exposure faces south at both localities.

Few specimens of larger mammals (greater than 2 kg body weight; about rabbit-sized) are present in the collections, and most of these are fragments of teeth and bone that cannot be identified below family level. The recognizable larger mammals are a mustelid, a merycoidodont and an equid.

AGE

There are no radiometrically datable beds within the Harrison Formation in Cherry County. However, volcanic ashes near the stratigraphic center of the formation in Sioux County, near its type area, have been fission-track dated at 21.9 and 20.7 mya (Tedford et al., 1987). The age of the fauna described here is believed to be very close to the dates obtained from elsewhere in the Harrison Formation. These dates indicate an early Miocene or late Arikareean age for the Harrison Formation (Berggren et al., 1984).

Tedford et al. (1987:184–185, 193–194) defined informal early and late divisions of the Arikareean, and suggested that both early and late phases of these divisions might be possible with future additions to the known faunas from these levels. However, in their figure (Tedford et al., 1987:fig. 6.3), they listed taxa at the boundaries of all of the early and late phases of the Arikareean. In another figure (Tedford et al., 1987:fig. 6.2), they placed the Harrison fauna (and the formation) entirely within the early phase of the late Arikareean. Unfortunately, the taxa utilized by Tedford et al. (1987) to separate the late from the early Arikareean were not small mammals (rodents, insectivores, marsupials). The only mention of rodents in their definition of the late Arikareean is limited to the late phase, including only the first occurrence of *Mylagaulodon,* greatest diversity of palaeocastorine beavers, and last occurrence of entoptychine geomyids.

Fisher and Rensberger (1972) divided the late Oligocene–early Miocene John Day Formation into concurrent-range zones. These zones have been correlated subsequently to Arikareean faunas from both the Great Plains and Rocky Mountain areas (Rensberger, 1973, 1979, 1980; Tedford et al., 1987). Based on Fisher and Rensberger's criteria, the presence of both *Entoptychus* and *Gregorymys* puts the McCann Canyon local fauna within the *Entoptychus–Gregorymys* concurrent-range zone, which Tedford et al. (1987:fig. 6.2) have correlated with the latest part of the late phase of the early Arikareean and the majority of the late Arikareean.

DENTAL TERMINOLOGY AND MEASUREMENTS

The dental terminology used below for rodents is basically that of Wood and Wilson (1936), with modifications for the geomyoids (Rensberger, 1971) and mylagaulids (Rensberger, 1979). Lagomorph dental terminology follows that of Wood (1940) and Dawson (1958). The dental terminology for the marsupials and insectivores follows that of Van Valen (1966).

All dental measurements represent maximum measurements taken at the base of the enamel in brachydont species (see Rich and Rasmussen, 1973:fig. 1 for diagram of dimensions of insectivore teeth), at the maximum dimension in mylagaulids (about mid-crown height), and at the occlusal surface in *Entoptychus* and *Archaeolagus.*

Abbreviations for dental measurements are: a-p, anteroposterior length; tr, transverse width; tra, anterior transverse width (trigonid width in insectivore lower molars, metalophid or protoloph width in rodents); trp, posterior transverse width (talonid width in insectivores, hypolophid or metaloph width in rodents). Additional abbreviations for statistical parameters and crown height in mylagaulids are listed in the appropriate tables.

SYSTEMATIC PALEONTOLOGY

Order Marsupialia Illiger, 1811

Family Didelphidae Gray, 1821

Herpetotherium Cope, 1873

Crochet (1977) distinguished North American Tertiary didelphids of the tribe Didelphini as belonging to a genus separate from *Peratherium,* the Tertiary European didelphine, based mainly on the size and arrangement of stylar cusps on the upper molars. Recently, Krishtalka and Stucky (1983) rejected this distinction because of the variable nature of these features in Eocene species, but retained the type species of *Herpetotherium, H. fugax,* in the genus because of the distinct morphology of the anterior dentition as defined by Fox (1983).

All of the Oligocene and later Tertiary didelphines from North America are characterized by an enlarged central stylar cusp on the upper molars, and a reduced or absent stylar cusp B (Stock and Furlong, 1922; Hough, 1961; Green and Martin, 1976; Korth, in press). These are diagnostic features of *Herpetotherium* as redefined by Crochet (1977), which is thus distinguished from the Old World *Peratherium,* which has a dominant stylar cusp B on the upper molars with a reduced or absent cusp D and cusp C. One specimen referred below to *Herpetotherium youngi,* UNSM 24195 (Fig. 3E), preserves the alveoli for I_3 and I_4, showing that these teeth are enlarged and anteriorly projecting as in *H. fugax.* Therefore, the later Tertiary North American species of didelphines are referred to *Herpetotherium,* based on consistency of size of the stylar cusps on the upper molars, and their association with the morphology of the lower incisors.

Herpetotherium youngi (McGrew, 1937)
(Fig. 3, Table 2)

Peratherium youngi McGrew, 1937.
Peratherium spindleri J. R. Macdonald, 1963.
Peratherium species indeterminate: J. R. Macdonald, 1970.
Peratherium cf. *spindleri*: Green and Martin, 1976.

Referred specimens.—UNSM 24186, 24187, 24189, 24191, and 24195, mandibles with lower cheek teeth; UNSM 24200, maxilla with LM^2–M^3; UNSM 24188, 24190, 24196, 24197, 24201, and 24202, isolated cheek teeth.

Description.—The antemolar dentition of *H. youngi* has not been described previously. The description provided here is based on UNSM 24195.

Alveoli for at least two incisors preserved anterior to canine alveolus; both smaller than the canine alveolus, laterally compressed, and inclined anteriorly; anterior alveolus larger than the posterior one. Alveolus for C_1 large, oval, opening anterodorsally; extending posteriorly to below P_2.

P_1 small, laterally compressed, and single rooted; single cusp along anterior margin of tooth; low, sloping crest extending posteriorly to minute heel. P_2 two-rooted; single major cusp (?protoconid); distinct talonid comprising posterior one-third of tooth; talonid wider than anterior two-thirds of tooth.

P_3 subequal in length to P_2; major trigonid cusp (?protoconid) extending dorsally higher than cusps of molars; minute cuspule (?paraconid) on anterior slope of protoconid on unworn specimen; talonid wider than trigonid; minute cusp (?entoconid) present on posterolingual corner of talonid.

Short diastema between P_1 and P_2 on all observable specimens; large mental foramen below diastema; smaller posterior mental foramen below anterior root of M_1.

Discussion.—Green and Martin (1976) reviewed middle Tertiary species of didelphines from the Great Plains. They argued that *Peratherium spindleri* from

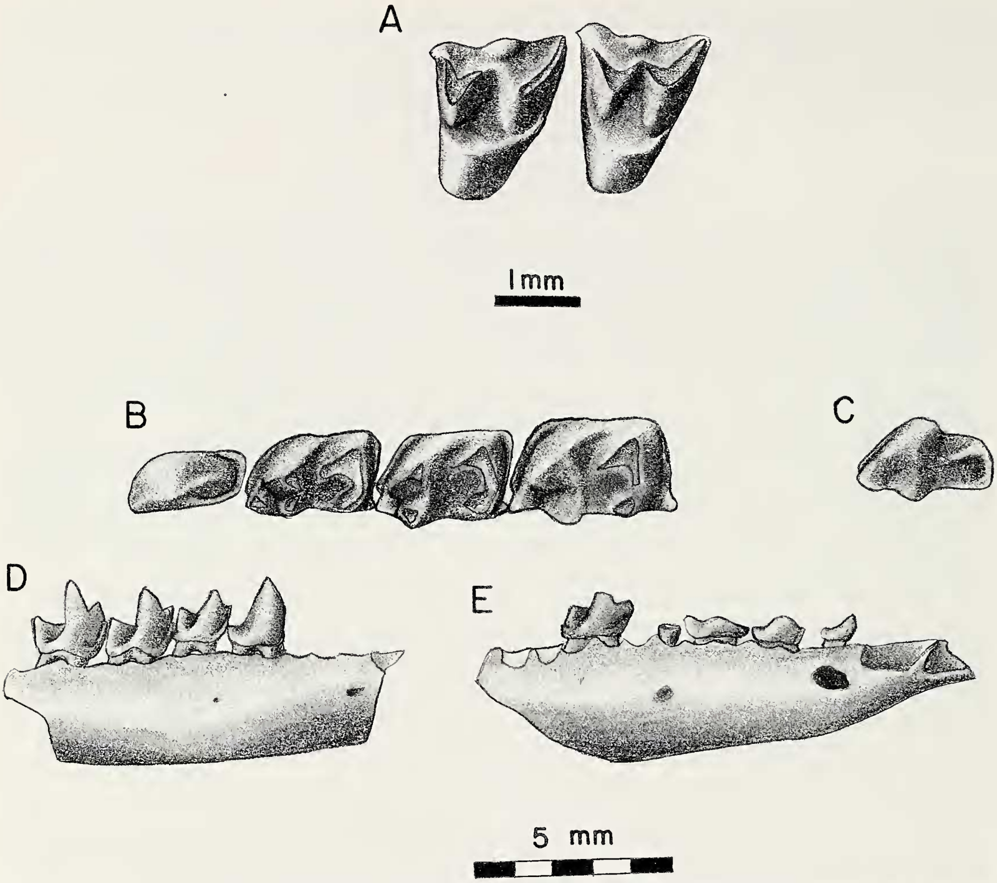

Fig. 3.—Dentitions of *Herpetotherium youngi.* A, UNSM 24200, partial maxilla with LM^2–M^3. B, UNSM 24186, RP$_3$–M$_3$. C, UNSM 24187, RM$_4$. D, UNSM 24186 (same as B), lateral view of mandible. E, UNSM 24195, lateral view of mandible with RP$_1$–M$_1$.

the Sharps Formation of South Dakota was very likely synonymous with *P. youngi* but did not synonymize the two species due to lack of material (*H. youngi* was known from two isolated teeth). With available material from Cr-117 and Cr-125, it is evident that the lower dentition is indistinguishable from the holotype of *H. spindleri,* and the upper molars are clearly conspecific with the holotype of *H. youngi.* Therefore it is appropriate to synonymize these two species following the arguments of Green and Martin (1976).

The size of the UNSM specimens of *H. youngi* (Table 2) is nearest that of specimens cited by Green and Martin (1976:table 1) from the Sharps, Monroe Creek, and Harrison formations. *H. youngi* is slightly smaller than Orellan *H. fugax,* and slightly larger than specimens of Hemingfordian age. The only other Arikareean didelphine is *H. merriami* from the John Day Formation (Stock and Furlong, 1922), which is larger than *H. youngi.*

McGrew (1937) described the holotype of *H. youngi* as an M^3, an identification followed by subsequent authors. However, the specimen (UC 1544) is more likely an M^2. In didelphids, M^3 is buccolingually elongate and more nearly symmetrical about a central transverse axis than are M^1 and M^2. UC 1544 is less symmetrical

Table 2.—*Dental measurements of* Herpetotherium youngi *from the Harrison Formation, Nebraska.* * = *measurement taken from Green and Martin (1976:fig. 6f). Measurements in mm.*

UNSM no.		24186	24187	24188	24189	24190	24195	24196	24197
P_1	a-p				0.95		0.88		
	tr				0.44		0.41		
P_2	a-p				1.48		1.16		
	tr				0.67		0.60		
P_3	a-p	1.42							1.65
	tr	0.66							0.77
M_1	a-p	1.50						1.81	1.85
	tra	0.90						1.07	1.03
	trp	0.94						1.02	1.10
M_2	a-p	1.60		1.74			1.72	2.04	1.84
	tra	1.05		0.91			1.02	1.28	1.36
	trp	1.13		1.00			1.08	1.24	1.07
M_3	a-p	1.95				1.99			
	tra	1.14				1.11			
	trp	1.14				1.10			
M_4	a-p		1.68			1.90			
	tra		0.85			0.98			
	trp		0.62			0.65			

UNSM no.		24197	24200	24201	24202	UC 1544 Type*
M^1	a-p				1.55	
	tr				1.79	
M^2	a-p		1.67			1.74
	tr		2.00			1.86
M^3	a-p	1.63	1.60	1.63		
	tr	2.11	1.99	2.21		

than typical M^3s of didelphines and more nearly approaches the outline seen in M^2 (see Green and Martin, 1976, for appropriate comparative figures).

Order Insectivora Illiger, 1811
Family Geolabididae McKenna, 1960
Centetodon Marsh, 1872
Centetodon divaricatus, new species
(Fig. 4C–F)

Holotype.—UNSM 24170, LM^2.

Referred specimens.—UNSM 24171, partial mandible with LP_3 and alveoli for P_1 through M_1; UNSM 24191, partial mandible with LM_1.

Type locality.—UNSM locality Cr-117.

Diagnosis.—Largest species of the genus; distinct lingual emargination on upper molars; lingual roots on upper molars more widely divergent than in other species; anterior mental foramen on mandible anterior to P_2, farther anterior than in any other species; diastema between P_1 and P_2, unknown in other species.

Etymology.—Latin, *divaricatus*, spread apart.

Description.—Holotype (UNSM 24170) very similar in occlusal morphology to M^2 of *C. chadronensis* and *C. marginalis* (Lillegraven et al., 1981) but larger than any specimen of *C. magnus*, the largest

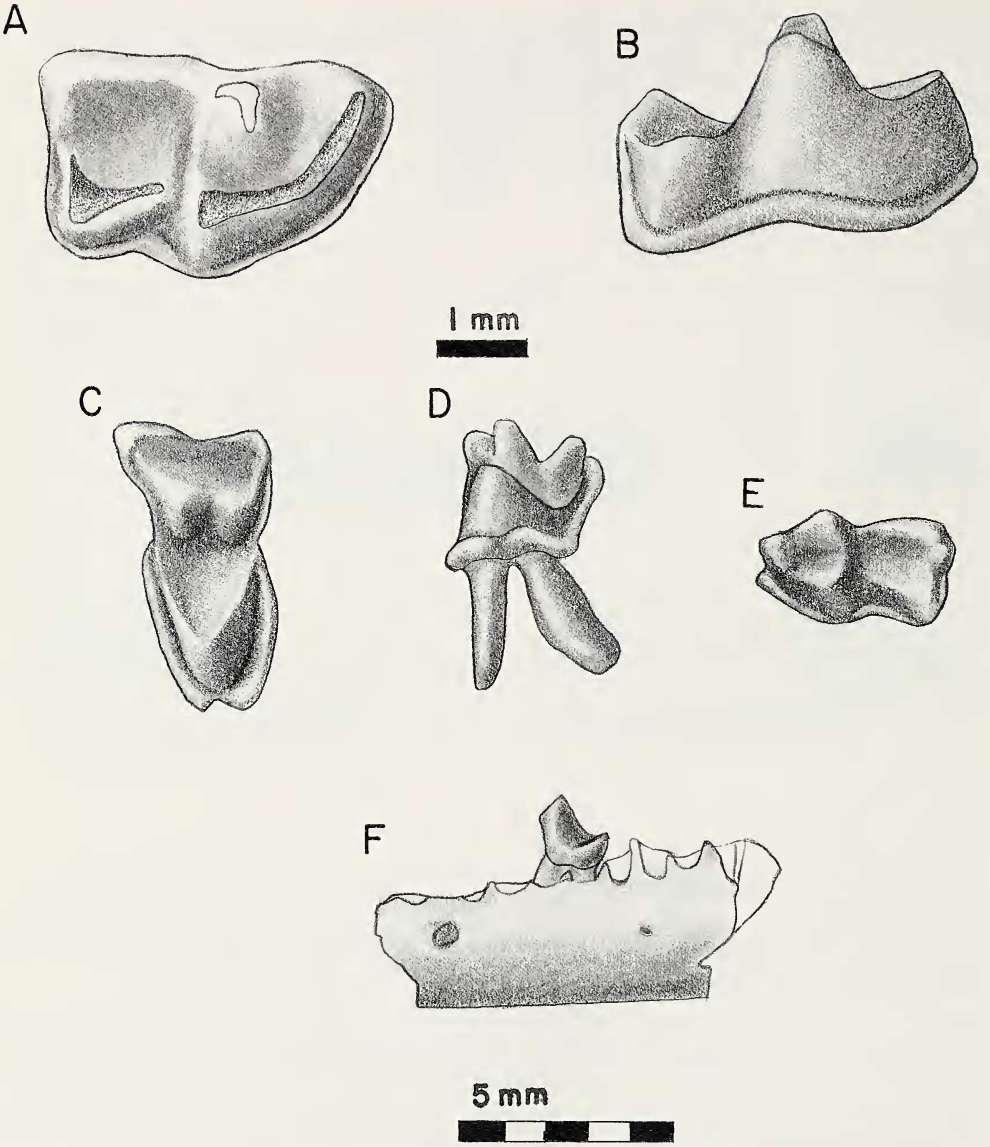

Fig. 4.—Dentitions of *Ocajila* sp. and *Centetodon divaricatus* from the Harrison Formation of Nebraska. A, B, *Ocajila* sp., UNSM 24166, M_1. A, Occlusal view. B, Buccal view. C–F, *Centetodon divaricatus.* C, D, UNSM 24170 (holotype), LM^2. C, Occlusal view. D, Lingual view. E, UNSM 24191, LM_1. F, UNSM 24171, lateral view of mandible with LP_3.

previously reported species (a-p, 1.78 mm; tra, 3.30 mm; trp, 3.10 mm); parastyle, preparacrista, and postmetacrista well developed; conules absent; anterior and posterior cingula broad shelves, extending approximately one-half width of tooth from lingual margin; both cingula extend lingual to protocone, producing distinct lingual emargination; lingual roots widely divergent; distance between apices of roots nearly twice lingual length of tooth.

P_3 as in other species of *Centetodon*; laterally compressed, large (a-p, 1.64 mm; tra, 0.72 mm; trp, 0.68 mm); large protoconid; minute cuspule (?paraconid) on anterolingual slope of protoconid; talonid small, no distinguishable cusps; distinct cristid running posteriorly from apex of protoconid to posterior tip of talonid along buccal side: small buccal cingulid running one-half length of tooth from talonid anteriorly.

Alveoli for C_1, P_1, P_2, P_4 and M_1 preserved in UNSM 24171; alveolus for C_1 large, laterally compressed oval; P_1 and P_2 two rooted; P_2 slightly larger than P_1. M_1 differs from specimens of *C. chadronensis* and *C. marginalis* only in its larger size (a-p, 2.21 mm; tra, 1.28 mm; trp, 1.21 mm).

Discussion.—Centetodon divaricatus is easily distinguishable from other species of the genus by its larger size. The lingual roots of the upper molars are widely spread as in *C. marginalis* and *C. wolffi.* The anterior and posterior lingual cingula on the upper molars are very broad. This character is variable in several species of *Centetodon* (Lillegraven et al., 1981), but appears better developed in *C. divaricatus* than in specimens of any other species previously figured. The lingual cingulum on the upper molars is not confluent around the base of the protocone as in *C. kuenzii* (Lillegraven and Tabrum, 1983); rather, the anterior and posterior cingula are widely separated. The deep lingual emargination between the anterior and posterior cingula on M^2 of *C. divaricatus* is much more marked than in specimens of *C. marginalis.*

P_3 of *C. divaricatus* is aligned directly anteroposteriorly. This orientation of P_3 is also present in *C. magnus,* and differs from that in other species, in which P_3 is positioned obliquely with the anterior end pointing slightly lingually.

Two features of the mandible also separate *C. divaricatus* from other species of the genus: the position of the anterior mental foramen and the presence of a diastema anterior to P_2. In other species of *Centetodon* the anterior mental foramen is positioned between the anterior root of P_2 and the anterior root of P_3 (Lillegraven et al., 1981:30). In *C. divaricatus* it is well anterior to P_2. Anterior to P_2 in *C. divaricatus,* above the mental foramen, is a distinct diastema. This diastema in UNSM 24171 is much larger (0.90 mm) than in any figured species of *Centetodon* (Lillegraven et al., 1981).

Centetodon divaricatus from the Harrison Formation represents the latest occurrence of the genus. Previously, the latest occurrence of *Centetodon* was based on specimens from the Monroe Creek Formation, South Dakota (Lillegraven et al., 1981:105), questionably referred to *C. magnus.* If Lillegraven et al. (1981) based their identification on size, it is possible that the specimens are referable to *C. divaricatus.* Besides being the youngest species of the genus, *C. divaricatus* is the most derived species in size, development of lingual cingula, and divergence of the lingual roots of the upper molars.

Family Soricidae Gray, 1821
Domnina Cope, 1873
Domnina sp.
(Table 3)

Referred specimen.—UNSM 24169, partial mandible with LM_1–M_3.

Locality.—UNSM locality Cr-125.

Discussion.—UNSM 24169 is smaller than the two species of *Domnina* known from the Sharps fauna of South Dakota and the Orellan species of the genus. It is larger than the unnamed Arikareean species described by Repenning (1967:9–10) from California. It most closely approaches Chadronian *D. thompsoni* in size (Simpson, 1941; Table 3, this paper).

The lingual cusps of M_1 and M_2 on UNSM 24169 are broken away, thus eliminating the entostylids, the morphology of which separates the Arikareean species from the earlier Oligocene species of the genus (J. R. Macdonald, 1963, 1970; Hutchison, 1972). No species determination can be made on the specimen due to its fragmentary nature.

Table 3.—*Dental measurements of* Mystipterus, Scalopoides *sp., and* Domnina *sp. from the Harrison Formation, Nebraska. Measurements in mm.*

	M_1			M_2			M_3		
	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp
Mystipterus sp.									
UNSM 24178	1.38	1.10	1.18	1.65	1.24	1.18			
Scalopoides sp.									
UNSM 24192	1.59	0.97	1.21						
Domnina sp.									
UNSM 24169	2.00	—	1.23	1.56	1.22	1.13	—	0.93	—

Family Talpidae Gray, 1821
Subfamily Talpinae Fischer von Waldheim, 1817
Scalopoides Wilson, 1960
Scalopoides sp.
(Fig. 5A, B)

Referred specimen.—UNSM 24192, partial mandible with LM_1.

Locality.—UNSM locality Cr-117.

Description.—The M_1 of UNSM 24192 is smaller than any other recorded for *Scalopoides* (a-p, 1.64 mm; tra, 0.93 mm; trp, 1.14 mm; Wilson, 1960:44; Hutchison, 1968:table 12). As in *S. isodens* the paracristid is straight, leaving the trigonid widely open lingually. It is not deflected posteriorly as in *S. ripafodiator.* The cristid obliqua of UNSM 24192 does not extend as far lingually as on M_1 in the other species. A small mental foramen is present in the mandible ventral to a point between P_4 and M_1.

Discussion.—UNSM 24192 is separable from *Mystipterus* of the McCann Canyon fauna by its larger size, greater development of the entocristid, and shape of the trigonid on M_1.

UNSM 24192 is very close in morphology to specimens of *Scalopoides isodens* from the Hemingfordian of Colorado, differing only in being about 20% smaller. Too little material is known to establish a new species from the Arikareean. It is possible that UNSM 24192 lies within the size range of *S. isodens,* which is also known from few specimens.

Scalopoides from the McCann Canyon fauna is the earliest record of this genus.

Subfamily Uropsilinae Dobson, 1883
Mystipterus Hall, 1930
Mystipterus sp.
(Fig. 5C, D; Table 3)

Referred specimen.—UNSM 24178, partial mandible with LM_1–M_2.

Description.—Equal in size to *M. martini* (Wilson, 1960:40); mandible slender; small mental foramen below alveolus for posterior root of P_4, slightly more anterior than in described species; M_2 slightly larger than M_1; trigonid of M_1 narrower than talonid; anterior cingulid and paraconid broken; posterior

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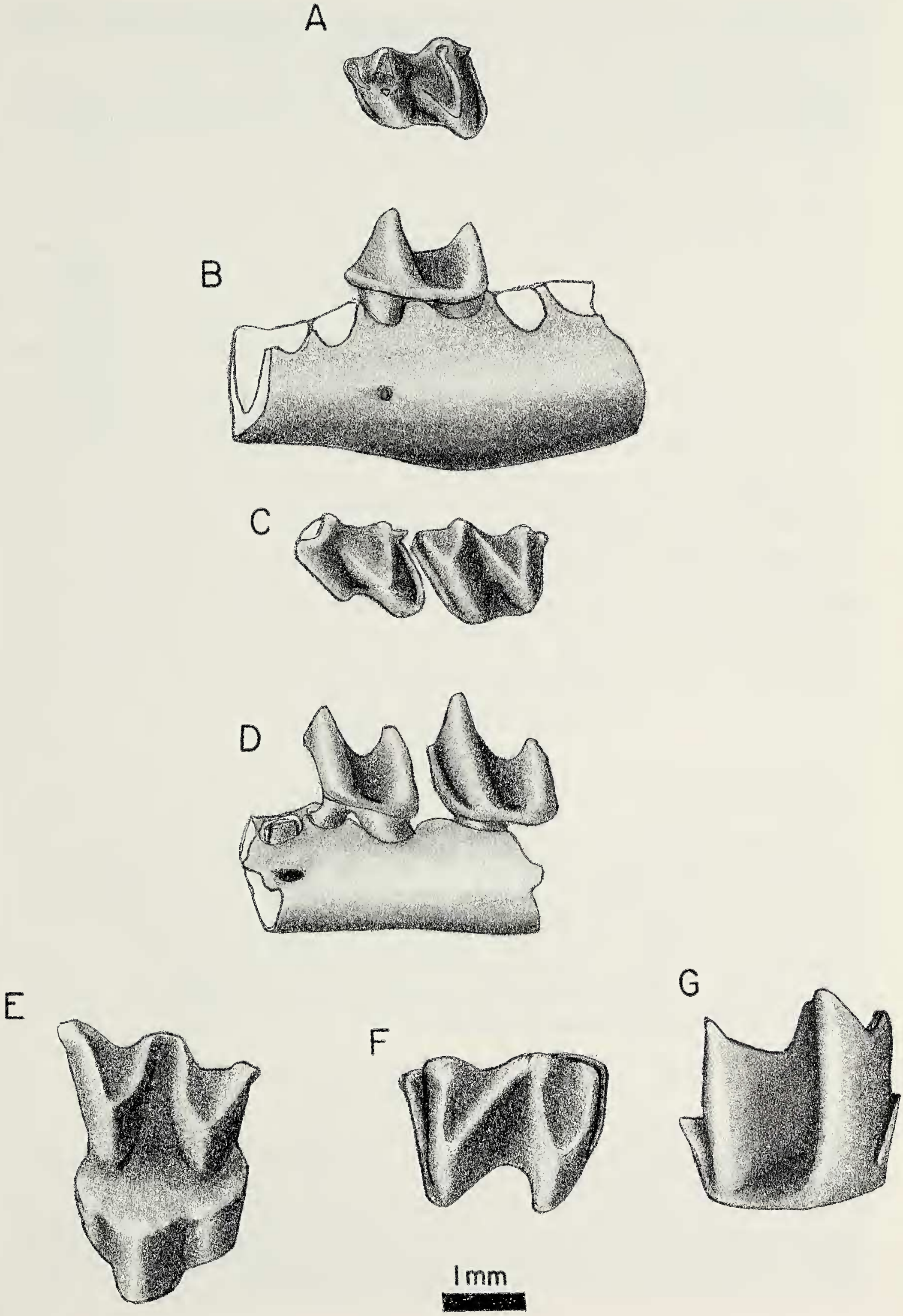
Fig. 5.—Talpidae and Proscalopidae from the Harrison Formation, Nebraska. A, B, *Scalopoides* sp. UNSM 24192. A, Occlusal view, M_1. B, Lateral view of mandible. C, D, *Mystipterus* sp., UNSM 24178. C, Occlusal view, M_1–M_2. D, Lateral view of mandible. E–G, *Proscalops secundus.* E, UNSM 24185, LM^2. F, G, UNSM 24179, RM_2. F, Occlusal view. G, Buccal view.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1mm

cingulid present; no cingulid on buccal sides of protoconid and hypoconid; protoconid largest cusp of trigonid; cristid obliqua joins trigonid lingual to protoconid; hypoconulid projecting directly posteriorly from base of entoconid; no entocristid present, leaving talonid open lingually.

M_2 trigonid wider than talonid; anterior cingulid narrow shelf along base of anterior face of trigonid; paraconid smallest cusp of trigonid, obliquely compressed; protoconid large, crescentic, as in M_1; no cingulid on buccal sides of protoconid or hypoconid; entoconid as in M_1; cristid oblique joins trigonid at base of metaconid; talonid more anteroposteriorly compressed than in M_1; rudimentary entocristid originating from entoconid, ending anteriorly half way to metaconid.

Discussion.—UNSM 24178 is assigned to *Mystipterus* based on Hutchison's (1968:36) emended diagnosis, which includes the character's small size, moderately brachydont cheek teeth, anterior and posterior buccal cingulids present on lower molars, and trigonid cusps of M_1 crowded together. The only diagnostic character listed by Hutchison not present in UNSM 24178 is a developed entocristid on the lower molars, which appears to be a variable trait in the genus.

Differences in the lower molars and mandible between UNSM 24178 and other species of the genus (poorly developed buccal cingulids and entocristid, more anterior position of mental foramen) are here considered primitive. There is no character of molar morphology that would preclude considering the species represented by UNSM 24178 as the ancestor of the later Tertiary species. Hutchison (1968) suggested that a common ancestor for *Mystipterus* (previously known from Hemingfordian to Clarendonian rocks) would probably be found in the early Miocene. Hence, UNSM 24178 from the Harrison Formation also appears to fit the temporal requirements for ancestry of the genus.

Hutchison (1968) recognized two subgenera of *Mystipterus, Mystipterus* and *Mydecodon,* based on the antemolar dentition. Because this part of the dentition is not preserved in UNSM 24178, it cannot be definitely referred to a subgenus.

Family Proscalopidae Reed, 1961
Proscalops Matthew, 1901
Proscalops secundus Matthew, 1909
(Fig. 5E, F; Table 4)

Referred specimens.—UNSM 24179, 24180, 24182 to 24185, isolated cheek teeth; UNSM 24181, two right humeri.

Discussion.—*Proscalops secundus* is known elsewhere from the Monroe Creek Formation in South Dakota (Matthew, 1909; Galbreath, 1953; J. R. Macdonald, 1963, 1970). The specimens referred here differ from *P. evelynae* (Sharps Formation) in the stronger development of the metastylid on M_2, the stronger "V"-shape of the paracone on M^2, and the pinching of the protocone on the upper molars (Barnosky, 1981). Two talpoid humeri from Cr-125 are identical to those of proscalopids (Barnosky, 1981:fig. 17, 18) and probably represent *P. secundus* based on their association with the teeth.

Family Erinaceidae Fischer von Waldheim, 1817
Ocajila Macdonald, 1963

Type species.—*Ocajila makpiyahe* Macdonald, 1963.

Range.—Early Arikareean (latest Oligocene) of South Dakota, and possibly late Arikareean (earliest Miocene) of Nebraska.

Discussion.—J. R. Macdonald (1963) based *Ocajila makpiyahe* on a mandible with M_2–M_3 (SDSM 56105) from the early Arikareean Sharps Formation in South Dakota. Later (J. R. Macdonald, 1970), he referred two other specimens to this species. No other species have been assigned to this genus.

Table 4.—*Dental measurements of* Proscalops secundus *from the Harrison Formation, Nebraska. Measurements in mm.*

	M_1			M_2		
UNSM no.	a-p	tra	trp	a-p	tra	trp
24179				2.67	2.13	1.86
24180	2.76	1.63	1.92			

	M^1		M^2		M^3	
	a-p	tr	a-p	tr	a-p	tr
24183			2.45	3.62		
24185	2.23	3.94				
24185	2.81	3.57				
24185	2.92	3.55				
24185	2.51	3.48				
24185			2.27	3.30		
24185			2.48	3.45		
24185					2.13	2.12

Eaton (1985:fig. 5B) identified a single specimen (UW 14024) as "cf. *Ocajila* sp." from the middle Eocene Wiggins Formation, Wyoming. This specimen has an M_1 very similar to that of the later Tertiary genus *Lanthanotherium.* The molars in the Wyoming specimen decrease in size posteriorly as in *Lanthanotherium* and *Ocajila.* The trigonids of the last two molars of UW 14024 are much more open lingually than in *Ocajila* or *Lanthanotherium,* and the paracristid is much higher than in the type species of *Ocajila.* Specimens from the middle Eocene Badwater fauna of Wyoming identified as "Erinaceid sp." are of equal size, have these features (Krishtalka and Setoguchi, 1977:fig. 4A, B), and may be referable to the same species as UW 14024.

The most thorough discussion of the relationships of *Ocajila* (Engesser, 1979) noted little or no difference between the holotype of *O. makpiyahe* and younger species from North America referred to *Lanthanotherium.* Engesser (1979) found that molars of the European species and the North American species of *Lanthanotherium* differed only in size, the European species being larger. The anterior dentition of North American and European species of *Lanthanotherium,* however, is markedly different (James, 1963). Engesser (1979) suggested that the North American species referred to *Lanthanotherium* might be placed in *Ocajila,* and the European species retained in the former based on the difference in the anterior dentition. He did not make this separation formally because the anterior dentitions of *O. makpiyahe,* type species of the genus, and of some of the European species were not known.

Ocajila sp.
(Fig. 4A, B)

Referred specimen.—UNSM 24166, RM_1.

Description.—UNSM 24166 relatively large for an erinaceid (a-p, 4.07 mm; tra, 2.28 mm; trp, 2.21 mm); trigonid longer and wider than talonid; protoconid and metaconid highest cusps on tooth; paracristid runs anteriorly from protoconid, sloping ventrally to paraconid; trigonid widely open lingually; talonid with two subequal cusps, entoconid and hypoconid; cristid obliqua runs directly anteriorly from hypoconid, joining trigonid posterior and just lingual to base of protoconid; cingulid continuous from below paraconid to center of posterior wall of talonid along buccal side of tooth, rising to meet talonid basin at its posterior end.

Discussion.—The M_1 referred here to *Ocajila* sp. is similar to M_1s referred to *Lanthanotherium* from the later Tertiary of California, Oregon and Europe (Lindsay, 1972:fig. 4; James, 1963:fig. 19; Engesser, 1979:plate 2). UNSM 24166 is larger than any of the North American species referred to *Ocajila* or *Lanthanotherium,* and smaller than most European species (J. R. Macdonald, 1963:167; James, 1963:table 9; Lindsay, 1972:table 3).

The holotype of *O. makpiyahe* does not have an M_1; therefore, no direct comparison can be made with UNSM 24166. UNSM 24166 probably represents a new species based on its large size.

Amphechinus Aymard, 1850
Amphechinus sp.

Referred specimen.—UNSM 24198, LP_4.

Locality.—UNSM locality Cr-125.

Description.—UNSM 24198 closely resembles P_4 of *Amphechinus ironcloudi* (J. R. Macdonald, 1970:20; Rich and Rasmussen, 1973:23) but is larger (a-p, 3.07 mm; tra, 1.68 mm; trp, 2.00 mm); protoconid largest cusp; paraconid well developed, larger than metaconid, separated from protoconid by deep valley; trigonid well formed and widely open lingually; talonid wider than the trigonid but very short (anteroposteriorly); posterior margin of tooth concave posteriorly; posterior cingulid small ridge along posterior margin of tooth.

Discussion.—UNSM 24198 is very similar to P_4s from elsewhere in the Arikareean of North America referred to *Amphechinus ironcloudi* (J. R. Macdonald, 1970). UNSM 24198 has a talonid wider than the trigonid, as in *A. ironcloudi,* but is approximately 15% longer anteroposteriorly than in any specimen of *A. ironcloudi* (Rich and Rasmussen, 1973:table 4). There are no other morphological differences between UNSM 24198 and specimens of *A. ironcloudi.*

Parvericius Koerner, 1940
Parvericius voorhiesi, new species
(Fig. 6, 7G, Table 5)

Holotype.—UNSM 24167, mandible with M_2–M_3.

Referred specimens.—UNSM 24168, mandible with RP_4–M_2; UNSM 24172, mandible with RI_1 and P_4; UNSM 24173, mandible with RI_1 and P_4; UNSM 24174, partial mandible with LP_4–M_1; UNSM 24175, partial mandible with LP_4; UNSM 24176, partial mandible with RM_3; UNSM 24177, LM^1; UNSM 24193, LM_1; UNSM 24194, partial mandible with LM_2; UNSM 26530, maxilla with LP^3–M^1.

Type locality.—UNSM locality Cr-117.

Diagnosis.—Near size of *P. montanus*; M_3 with continuous posterior cingulid; well-developed parastyle on P^4.

Etymology.—Patronym for M. R. Voorhies in acknowledgment of his many contributions to later Tertiary vertebrate paleontology of Nebraska.

Description.—Mandible narrow; small mental foramen below center of P_4; I_1 large, oval in cross-section, flattened medially; enamel extends to level of alveolus on I_1; three single alveoli anterior to P_4 (I_2, C_1, P_2); alveolus for P_2 smaller than anterior alveoli; I_2 and C_1 alveoli opening anterodorsally.

P_4 two-rooted; protoconid highest cusp of trigonid; metaconid small cuspule on posterolingual slope of protoconid connected by sharp crest; paraconid slightly lower than protoconid, separated from protoconid by deep, narrow valley; trigonid subequal in length and width to talonid (just slightly narrower; see Table 5); single small cuspule present on talonid, lingual to center of tooth along posterior margin; no distinct cingulid on tooth.

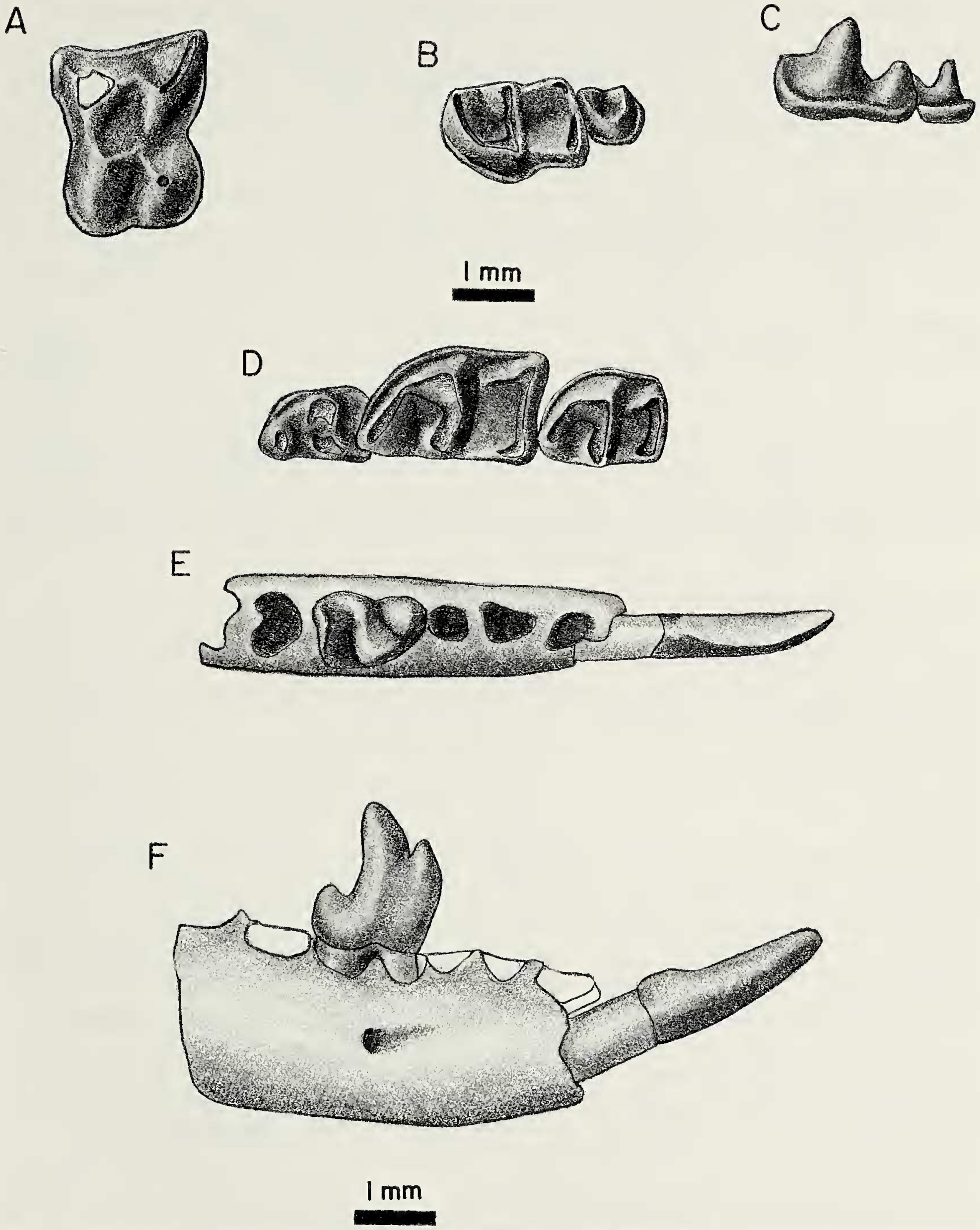


Fig. 6.—Dentitions of *Parvericius voorhiesi.* A, UNSM 24177, LM^1. B, C, UNSM 24167 (holotype), LM$_2$–M$_3$. B, Occlusal view. C, Buccal view. D, UNSM 24168, RP$_4$–M$_2$. E, F, UNSM 24172, partial mandible with RP$_4$ and I$_1$. E, Occlusal (dorsal) view. F, Buccal (lateral) view.

M$_1$ is larger than M$_2$ with anteroposteriorly compressed trigonid; proportions of anterior molars identical to those reported by Rich and Rasmussen (1973:39–40) for *P. montanus.*

Trigonid of M$_3$ longer than wide; paraconid set well anterior to metaconid, separated from protoconid by deep, sharp valley; protoconid largest trigonid cusp, closely appressed to metaconid; talonid lacking; small cingulid originating at buccal base of paraconid, wrapping around tooth along buccal side,

Table 5.—*Measurements of dentitions of* Parvericius voorhiesi. *Measurements in mm.*

UNSM no.		24167 TYPE	24168	24172	24173	24174	24175	24176	24193	24194
I_1	a-p			0.74	0.91					
	tr			0.58	0.62					
P_4	a-p		1.36	1.55	1.65	—	1.46			
	tra		0.89	0.72	0.88	0.86	0.92			
	trp		0.84	0.89	0.95	0.81	0.92			
M_1	a-p		2.30			1.98			1.96	
	tra		1.46			1.21			1.27	
	trp		1.49			1.12			1.21	
M_2	a-p	1.72	1.67							1.90
	tra	1.25	1.22							1.26
	trp	1.15	1.15							1.15
M_3	a-p	0.80						0.77		
	tr	0.77						0.57		

UNSM no.		26530	24193
P^3	a-p	1.30	
	tr	1.09	
P^4	a-p	2.19	
	tr	2.09	
M^1	a-p	2.15	2.00
	tr	2.38	2.42

continuing along posterior side of tooth to base of metaconid; tooth single rooted, root weakly bifurcated on holotype.

Rich and Rasmussen (1973) described the buccal half of P^3 of *P. montanus,* the remainder of the tooth being unknown. The buccal half of the P^3 of *P. voorhiesi* is identical to that of *P. montanus.* The lingual half of the tooth is much narrower (anteroposteriorly) than the buccal half. The only distinct cusp on the lingual half is the protocone which is a small conical cusp on the anterolingual edge of the tooth. Posterior to the protocone, there is a low sloping area that extends posterolingually.

P^4 of *P. voorhiesi* is nearly identical to that of *P. montanus* except that there is a well-developed parastyle at the end of the paracrista.

M^1 is equal in size and proportions to those of *P. montanus* (Rich and Rasmussen, 1973:table 6).

Discussion.—Parvericius voorhiesi differs from the type species, *P. montanus,* only in the presence of a posterior cingulid on M_3 and a well-developed parastyle on P^4. The species are otherwise indistinguishable. Rich and Rasmussen (1973) named *Stenoechinus tantalus,* another Arikareean erinaceid, that differs from *P. montanus* in only two features: morphology of M_3 (presence of posterior cingulid and second root), and proportions of M^1 (relatively wider than long). Whereas *P. voorhiesi* does have the posterior cingulid on M_3 as in *Stenoechinus* it is not as pronounced, and the tooth is not two-rooted. The upper molars of *P. voorhiesi* also do not have the proportions diagnostic of *Stenoechinus.*

Parvericius voorhiesi is the second species of this genus from North America. Specimens identified as *P. montanus* from the Monroe Creek Formation of South Dakota (L. J. Macdonald, 1972) may be *P. voorhiesi.* This is not certain because the diagnostic M_3 or P^4 is not known from that fauna. The only specimen figured as M_3 by L. J. Macdonald (1972:fig. 4D) is a marsupial M_4.

Order Rodentia Bowdich, 1821
Family Aplodontidae Trouessart, 1897
Subfamily Allomyinae Marsh, 1877
Alwoodia Rensberger, 1983
Alwoodia harkseni (Macdonald, 1963), new combination
(Fig. 7A–D; Table 6)

Allomys harkseni Macdonald, 1963.

Referred specimens.—UNSM 24005, maxillary fragment with RM^1 and M^2; UNSM 24088, LP^4; UNSM 24089, isolated upper molars; UNSM 24006, 24008, 24009, 24010, 24011, 24012, isolated upper and lower cheek teeth.

Emended diagnosis.—Equal in size to *A. magna*; minute lophule in central transverse valley of upper molars running posteriorly from paracone; fossettid posterior to mesoconid open on M_1, closed on M_2, M_3.

Description.—The only tooth not previously described for *A. harkseni* is P^4. As in P_4, upper premolar slightly larger than nearly all upper molars (none associated); anterocone large; buccal cusps crescentic; mesostyle large; protoloph not continuous; paracone isolated; protoconule obliquely compressed, connecting weakly to protocone; no accessory lophules in basins of teeth; protocone crest short, curving anteriorly; metaconule doubled, not connecting with protocone; minute cuspule attached to lingual metaconule; lingual metaconule much larger than buccal metaconule.

Discussion.—Rensberger (1983), in his description of the genus *Alwoodia* (type species *A. magna*) from the John Day Formation of Oregon, suggested that *Allomys harkseni* from South Dakota might be included in the new genus. He did not include it because the specimens previously referred to *A. harkseni* (J. R. Macdonald, 1963, 1970; L. J. Macdonald, 1972) probably represented more than a single species. This problem was also noted by Barnosky (1986). The aplodontid specimens from Cr-117 and Cr-125 can be divided into two distinct types. The larger, more lophate specimens are *A. harkseni,* and the smaller specimens are referred below to a new species of *Parallomys.*

Alwoodia harkseni is equal in size and lophodonty to the type species and can be referred easily to this genus based on the characters diagnosed by Rensberger (1983:43). The only differences between *A. magna* and *A. harkseni* are the presence of a minute lophule, arising from the paracone, in the central valley of the upper molars of *A. harkseni,* and the open fossettid posterior to the mesoconid on M_1. In *A. magna* there is no accessory lophule on the upper molars, and the fossettid posterior to the mesoconid is closed on all of the lower cheek teeth, not just the posterior two molars. In the only known P_4 of *A. harkseni* from South Dakota (SDSM 6273), the fossettid posterior to the mesoconid is closed lingually as in *A. magna* but is open buccally, unlike the opening in this fossettid on M_1 of *A. harkseni.*

Parallomys Rensberger, 1983
Parallomys americanus, new species
(Fig. 7E, F; Table 6)

Holotype.—UNSM 24000, isolated LM^1 or M^2.

Referred specimens.—UNSM 24001, 24002, 24003, 24004, 24007, 24087, all isolated lower cheek teeth.

Type locality.—UNSM locality Cr-117.

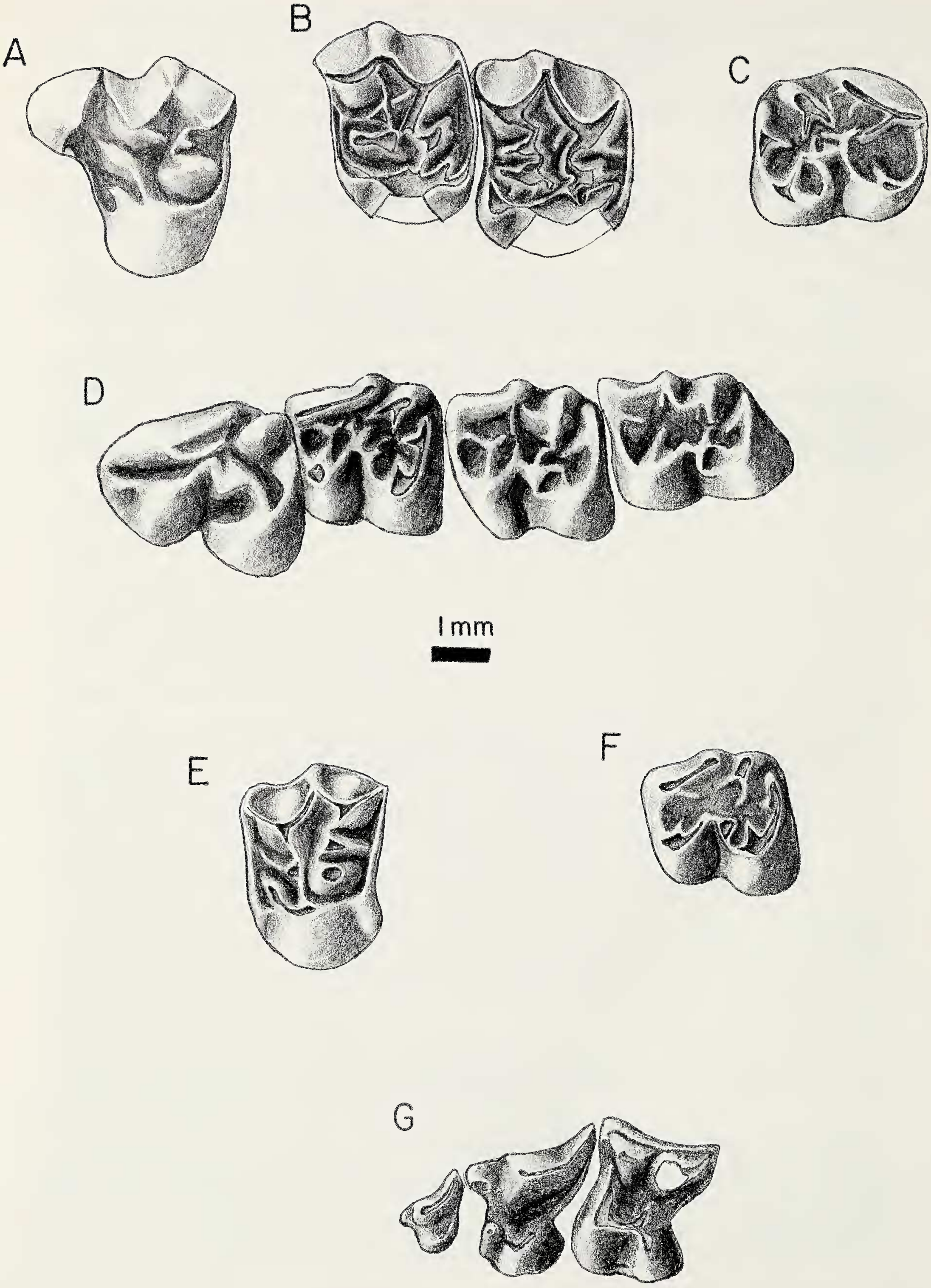

A
B
C
D
1mm
E
F
G

Table 6.—*Dental measurements of aplodontid and sciurid rodents from Cr-117 and Cr-125. Measurements in mm.*

	P_4			M_1 or M_2			M_3		
UNSM no.	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp
Parallomys americanus									
24004				2.23	2.10	2.01			
24003				2.31	1.97	2.19			
24001				2.23	1.80	2.24			
24007							2.97	2.19	1.97
Alwoodia harkseni									
24008				2.75	1.98	2.33			
24011				2.74	2.11	2.54			
							2.67	2.06	1.97
Nototamias quadratus									
24017	1.19	0.97	1.24	1.33	1.27	—			
24013				1.42	1.24	1.44			
24015				1.48	1.20	1.25			
Protosciurus sp.									
24090							3.12	2.61	2.63

	P^4		M^1 or M^2		M^3	
	a-p	tr	a-p	tr	a-p	tr
Parallomys americanus						
2400 (type)			2.20	3.05		
Allwoodia harkseni						
24088	3.20	3.29				
24005 (M^1)			2.38	3.05		
24005 (M^2)			2.42	3.08		
24006			2.60	3.38		
24009			2.48	3.07		
24010			2.54	3.17		
Nototamias quadratus						
24014	1.33	1.39 (d)				
24106			1.51	1.83	1.48	1.73
Protosciurus sp.						
	1.87	2.14	2.20	2.57		

Diagnosis.—Near size of *P. ernii*; buccal cusps on upper molars not as low-sloping as in European species; anteroposterior lophule from anteroconid on lower cheek teeth free posteriorly.

Etymology.—The trivial name indicates this is the only known North American species of this otherwise European genus.

Description.—Size of cheek teeth near that of *Parallomys ernii* (Rensberger, 1983:33; Table 6); accessory lophs on cheek teeth low and short; central transverse valley of upper molar simple without

←

Fig. 7.—Aplodontid rodents and *Parvericius voorhiesi* from the Harrison Formation, Nebraska and Sharps Formation, South Dakota. A–C, *Alwoodia harkseni* from Harrison Formation. A, UNSM 24088, LP^4. B, UNSM 24005, RM^1–M^2. C, UNSM 24011, RM_2. D, *A. harkseni* from Sharps Formation, SDSM 6273, LP_4–M_3. E, F, *Parallomys americanus* from Harrison Formation. E, UNSM 24000 (holotype), LM^1 or M^2. F, UNSM 24001, LM_1 or M_2. G, *Parvericius voorhiesi,* UNSM 26530, LP^3–M^1.

lophules; only lophule on upper molar anterior to protoconule, running anterobuccally; paracone and metacone crescentic, paracone more lingual than metacone; buccal metaconule smaller than lingual metaconule and buccolingually compressed; protoconule and lingual metaconule round; hypocone small.

Accessory lophules on lower molars short, shorter than in *Allomys cristabrevis* (Barnosky, 1986); small lophule running posteriorly into trigonid basin from metaconid or center of metalophulid I, ending without joining other lophules; short lingually running lophules from protoconid and mesoconid also free lingually; entoconid isolated with two small lophules, one running directly buccally or slightly posteriorly, other lophule running anteriorly and slightly buccal; hypoconulid large; anterior lophule of the hypoconid and posterior lophule of the mesoconid do not fuse to form fossettid; M_3 elongate posteriorly.

Discussion.—The weak development of lophs on the lower molars and the lack of accessory lophs in the basins of the cheek teeth of *P. americanus* make it referable to the otherwise European genus *Parallomys* and distinct from *Allomys* and other North American allomyines. The buccolingual compression and small size of the buccal metaconule on the upper molar of *P. americanus* most closely resemble the condition in *P. macrodon* among the European species.

Family Mylagaulidae Cope, 1881*a*

Promylagaulus McGrew, 1941

Type species.—*Promylagaulus riggsi* McGrew (1941).

Range.—Arikareean (latest Oligocene or earliest Miocene) of Nebraska and South Dakota.

Emended diagnosis.—Small mylagaulid; cheek teeth more hypsodont than *Meniscomys,* less hypsodont than *Mesogaulus*; P^4 with lingually expanded anterocone; occlusal outline oval in early stages of wear and more square in late stages of wear; four persistent fossettes on P^4 (posterolabial, posterolingual, anterolabial, anterolingual), anterolabial fossette commonly split anteriorly; P_4 with labial inflection large and expanded posteriorly with two small persistent fossettids (anterior and posterior); molars with dentine tracts on the anterior and posterior sides of the teeth; mesoconid and mesoconid spur lacking on lower molars.

Discussion.—Rensberger (1979) reviewed the genus *Promylagaulus,* and recognized the type species and three additional species. However, the large sample of specimens from Cr-117 and Cr-125 has led to the recognition of a second genus of mylagaulid (described below), to which all but the type species of *Promylagaulus, P. riggsi,* belong.

Rensberger (1979) provided a historical review of the phylogenetic relationships of *Promylagaulus* and concluded, contrary to previous authors, that it was not ancestral to later mylagaulids. His conclusions, however, were based mainly on the morphology of species referred here to a new genus (see below). Rensberger's (1979:17) conclusions for *Promylagaulus* are still applicable for both it and the new genus. *Promylagaulus,* based on the new referred material, has many features that are unlike those of the species of the new genus, and which make it a likely morphologic ancestor of the Hemingfordian "*Mesogaulus*" *novellus.*

The primitive features of *Promylagaulus* and the Promylagaulinae cited by Rensberger (1979, 1980; lower crown height, relatively smaller P^4_4 , early loss of the posterolabial fossette on P^4) do not eliminate it from an ancestral position, but clearly indicate its primitive morphology. However, Rensberger (1980) cited a number of characters of the promylagaulines that removed them from the ancestry of later mylagaulines (uninterrupted labial inflection on P_4; posterolabial compression of the hypocone on the molars; single fossette(-id) persists in molars).

Though the cheek tooth morphology of *Promylagaulus* and the new genus are distinct from one another, these two genera share one derived feature that is absent in *Crucimys*: the anterior fossettid on the lower molars is divided by the metalophule II. This feature is not known in any other mylagaulid.

Galbreath (1984) questioned the inclusion of *Mesogaulus novellus* in *Mesogaulus* based on the position of the anteroconid on P_4 (buccal rather than lingual) and the common separation of the lingual branch of the anterolingual fossette on P^4. "*Mesogaulus*" *novellus* also lacks a mesoconid crest on the lower molars which is present on the molars of other species of *Mesogaulus*. In two of these features "*M.*" *novellus* is similar to *P. riggsi*.

An accessory fossette on some specimens of P^4 of *P. riggsi* that occasionally fuses with the anterolabial fossette forming a "fork" at the anterior end of the fossette is also seen in "*Mesogaulus*" *novellus* (Black and Wood, 1956; Munthe, 1988). In later species of mylagaulines this forked fossette is always united and the lingual branch is never isolated (Gazin, 1932; Storer, 1975; Galbreath, 1984). The lower molars of *P. riggsi* lack the mesoconid crest, as in "*M.*" *novellus*. These shared characters appear to unite the latter two species and separate *novellus* from the genus *Mesogaulus*.

However, the teeth of "*M.*" *novellus* are higher-crowned and have a more complex pattern of fossettes(-ids) than do those of *P. riggsi*; therefore they are not congeneric. "*Mesogaulus*" *novellus* also has a strongly developed mesoconid crest on P_4 (this crest is lacking in promylagaulines), and the anterior fossettid of the molars is not divided as in *Promylagaulus* and the new genus. The development of the higher-crowned and more complex cheek teeth in "*M.*" *novellus* is viewed as a parallelism with *Mesogaulus* and the mylagaulines.

Promylagaulus and "*M.*" *novellus* are not directly ancestral to the mylagaulines (*Mesogaulus, Mylagaulus, Ceratogaulus, Epigaulus*), and neither is the new genus (Rensberger, 1979, 1980). The cladogram of relationships of the promylagaulines presented here (Fig. 8) is similar to the phylogeny of these rodents presented previously by Rensberger (1980:text-fig. 6).

Mylagaulodon angulatus from the Hemingfordian deposits of the John Day Formation (Sinclair, 1903) has frequently been suggested as the ancestor of the mylagaulines. However, the P^4 of this species (Nichols, 1976:fig. 8C) is not expanded anterolingually as in mylagaulines, *Promylagaulus* and the new genus, and is wider (buccolingually) than long (anteroposteriorly) as is the case in meniscomyines, particularly *Niglarodon* (Rensberger, 1981, 1983). *Mylagaulodon* may be a hypsodont meniscomyine and not a mylagaulid at all. The single isolated P^4 referred by Skwara (1988) to *Mylagaulodon* cf. *M. angulatus* (SMNH P1595.1) is identical to referred specimens of *Mesogaulus paniensis* from Colorado (Wilson, 1960:fig. 48) and should be included in that species. Likewise, the P^4 (FMNH P26266) from the Hemingfordian Rosebud Formation, South Dakota, described and figured by McGrew (1941:fig. 4, 10d) as *Mylagaulodon* cf. *angulatus*, is within the size range and morphology of P^4s of "*M.*" *novellus* (Black and Wood, 1956; Munthe, 1988) and should be referred to the latter species.

Promylagaulus riggsi McGrew, 1941
(Fig. 9A–E; Table 7)

Referred specimens.—From Cr-117 and Cr-125: UNSM 81004, maxilla with P^3–M^1; 81013–81016, 81021–81023, 81025, 81027–81030, 24130–24136, isolated P^4s; 81002, 81003, 81005–81007, 81011,

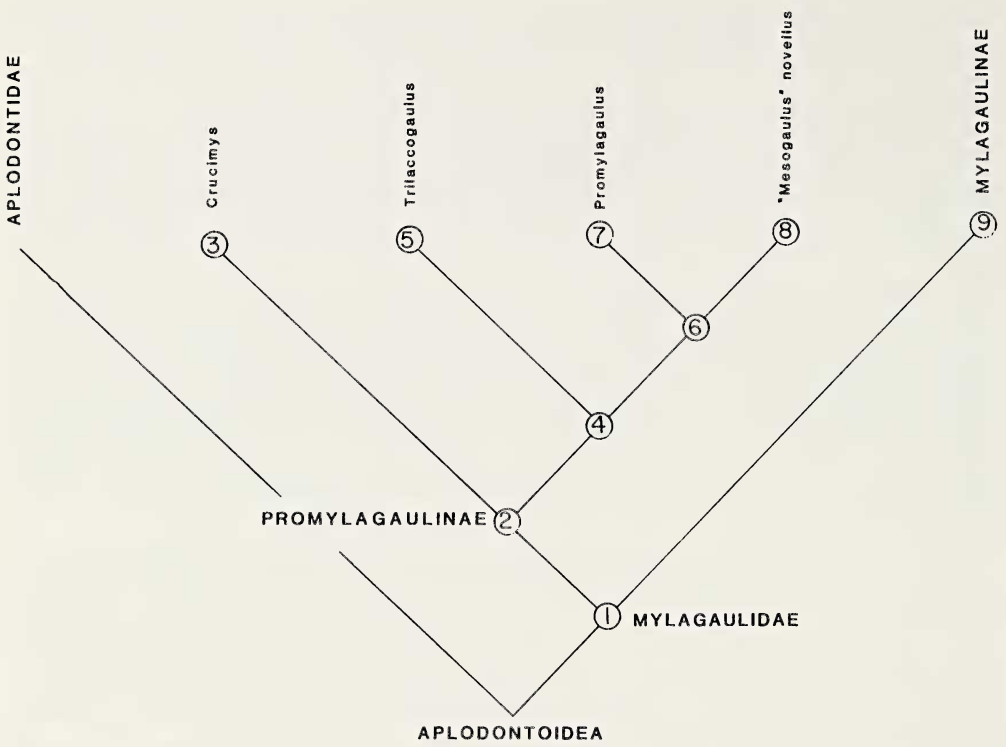


Fig. 8.—Cladogram of relationships of promylagauline mylagaulids. Explanation of nodes: 1. Mylagaulidae: subhypsodont to hypsodont cheek teeth, occlusal morphology lost in early wear, only series of enamel lakes remain; enamel failure on anterior and posterior margins of molars; P^4 much larger than molars; styles reduced or absent on upper teeth; anterocone of P^4 expanded lingually; incisors broad and gentle convex anteriorly; fossorial adaptations of skull and skeleton (see Wahlert, 1972, for additional cranial features). 2. Promylagaulinae: loss of mesoconid crest (=buccal mesolophid) on P$_4$, labial inflection deep posteriorly; molars wear to single, central fossette (-id); posterior labial fossette lost after moderate wear in P^4. 3. Mesolophid (=mesostylid crest) oriented directly transverse (not oblique) on lower molars. 4. Anterior fossettid of molars divided by metalophulid II. 5. Anterolingual fossette absent or very shallow on P^4; anterolabial fossette widened anteriorly (triangular in shape) on P^4; three fossettes persist on P$_4$. 6. Loss of mesoconid crest (=buccal mesolophid) on molars, labial inflection deep posteriorly; lingual branch of bifurcated anterolabial fossette on P^4 frequently isolated, minute fossette; fossettes of P^4 elongate (not ovate). 7. Lingual fossettid not developed on P$_4$, lingual inflection shallow. 8. Anteroconid on P$_4$ on buccal side of tooth; mesoconid crest (=buccal mesolophid) developed on P$_4$; greater hypsodonty; anterior fossettid on molars undivided; increased number of fossettes (-ids) on cheek teeth. 9. Mylagaulinae: Enhanced fossorial adaptations of skull and skeleton (also see Fagan, 1960; Wahlert, 1972); larger size; marked increase in hypsodonty and number of fossettes (-ids) on cheek teeth; anterior molars progressively lost with eruption of much enlarged premolar. See Rensberger (1975) and Wahlert (1972) for explanation of diagnostic characters of Aplodontoidea and Aplodontidae.

24137, 24138, mandibles with lower cheek teeth; 24139, 24140, 24147, isolated P$_4$s; 24141, 24143, 24146, isolated M$_1$ or M$_2$s.

Description.—Occlusal outline of P^4 oval in early stages of wear and more square in late stages of wear; posterolabial fossette smaller and less persistent than in other mylagaulids; anterolingual fossette persistent and anteroposteriorly elongate on unworn specimens, becoming oval to circular with wear; anterolabial fossette anteroposteriorly elongate and transversely narrow, widest anteriorly and oriented directly anteroposteriorly; posterolingual fossette expanded anteroposteriorly and directed labially

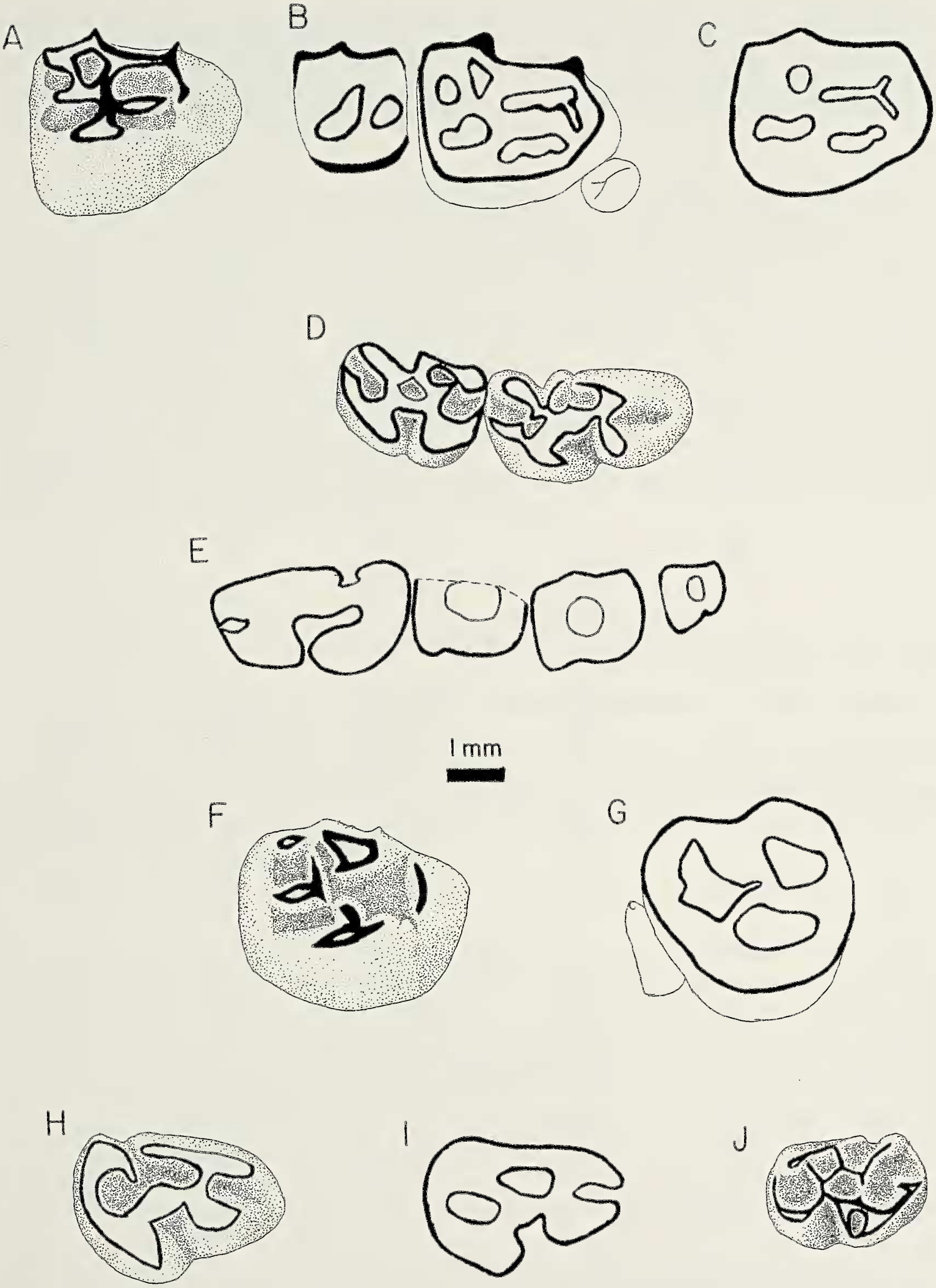


Fig. 9.—Mylagaulid rodents from the Harrison Formation. A–E, *Promylagaulis riggsi.* A, UNSM 81013, RP^4. B, UNSM 81004, RP^3–M^1. C, UNSM 81015, RP^4. D, UNSM 24137, RP$_4$–M$_1$. E, UNSM 81006, LP$_4$–M$_3$. F–J, *Trilaccogaulus ovatus.* F, UNSM 24152, RP^4. G, UNSM 24151, LP^3–P^4. H, UNSM 81009, RP$_4$. I, UNSM 81007, RP$_4$. J, UNSM 24142, LM$_1$ or M$_2$.

Table 7.—*Dental measurements of* Promylagaulus riggsi *and* Trilaccogaulus ovatus *from Cr-117 and Cr-125. Additional abbreviations: h, height of posterior dentine tract from highest lingual point on upper cheek teeth and lowest buccal point on lower cheek teeth; h/a-p, ratio of height of dentine tract to anteroposterior length (premolars); h/tr, ratio of height of dentine tract to transverse width (molars); N, number of individuals; M, mean; OR, range; S, standard deviation; CV, coefficient of variation. Measurements in mm.*

	N	M	OR	S	CV
			Promylagaulus riggsi		
P^4					
a-p	38	3.49	3.19–3.86	.17	5.0
tr	34	2.66	2.27–3.03	.20	7.4
h	34	2.01	1.31–2.76	.34	16.9
h/a-p	34	0.57	0.40–0.72	.09	15.6
P_4					
a-p	18	3.51	3.11–3.79	.16	4.7
tr	18	3.51	1.73–2.22	.11	5.5
h	14	1.78	1.33–2.68	.31	17.5
h/a-p	13	0.50	0.38–0.71	.09	17.3
M_1 or M_2					
a-p	23	2.09	1.86–2.37	.14	6.9
tr	20	1.70	1.51–1.81	.08	4.9
h	14	1.53	1.07–1.94	.27	17.4
h/tr	13	0.89	0.64–1.14	.15	17.2
			Trilaccogaulus ovatus		
P^4					
a-p	11	3.63	3.22–4.01	.24	6.7
tr	11	3.08	2.70–3.60	.30	9.7
h	6	2.78	2.51–3.20	.24	8.7
h/a-p	6	0.80	0.72–0.92	.07	8.4
P_4					
a-p	4	3.64	3.45–3.81	.13	3.6
tr	3	2.33	2.20–2.45	.10	4.4
h	4	1.99	1.85–2.06	.08	4.1
h/a-p	4	0.55	0.49–0.60	.04	7.2
M_1 or M_2					
a-p	8	2.35	1.86–2.69	.27	11.4
tr	8	1.81	1.58–1.94	.13	7.0
h	6	1.97	1.61–2.51	.28	14.3
h/tr	6	1.11	0.96–1.32	.13	11.8
			P. riggsi and *T. ovatus* undifferentiated		
M^1 or M^2					
a-p	30	2.08	1.88–2.32	.13	6.3
tr	28	2.05	1 88–2.18	.10	5.1
h	27	1.87	1.18–2.45	.38	20.4
h/tr	26	0.92	0.61–1.31	.19	20.6

toward the center of the tooth; variable presence of anterior central fossette which may fuse with anterolabial fossette to form a single "forked" fossette; ratio of height of posterior lingual enamel to anteroposterior length (h/a-p) ranging from 0.40 to 0.72 (mean = 0.57).

P_4 with labial inflection large and expanded posteriorly, closely appressed to the loph connecting mesoconid with metalophulid II and fusing with it in early wear, resulting in no lingual fossettid; lingual inflection deep with well-developed mesostylid; posterior fossettid small and disappears with moderate wear; anterior fossettid persistent but small; ratio of height of posterior buccal enamel to length of tooth (h/a-p) ranging form 0.38 to 0.71 (mean = 0.50).

Lower molars have the mesoconid and spur absent on all unworn to moderately worn specimens; metastylid crest strong, making anterolingual fossettid buccolingually compressed; labial inflection extending far posteriorly; ratio of height of posterior buccal enamel to width of tooth (h/tr) ranging from 0.64 to 1.14 (mean = 0.89).

Discussion.—The crown height of the cheek teeth of early mylagaulids has been determined by measuring the height of the dentine tract on the posterior side of the tooth and creating a ratio by dividing it by either the length (premolars) or the width (molars) of the tooth. On this basis, *P. riggsi* has lower crowned P^4s and lower molars than "*P.*" *ovatus* from Cr-117 and Cr-125 (see Table 7), but the lower premolars are of equivalent height. The height of the dentine tract is variable in all species measured and often has coefficients of variation ranging into the high teens. In the lower molars that can be separated into species based on occlusal morphology, the overlap of crown height ratios (h/tr) is nearly 40%, but the mean values are distinct (*P. riggsi* = 0.89; "*P.*" *ovatus* = 1.11). The crown height index for P_4 shows complete overlap for these two species. Only P^4 does not overlap in the range of this index (Fig. 10).

Trilaccogaulus, new genus

Type species.—*Trilaccogaulus lemhiensis* (Nichols, 1976).

Referred species.—*T. ovatus* (Rensberger, 1979) and *T. montanensis* (Rensberger, 1979).

Range.—Arikareean (latest Oligocene and earliest Miocene) of Idaho, Montana, South Dakota and Nebraska.

Diagnosis.—Small mylagaulids; hypsodonty equal to that of *Promylagaulus*; P^4 oval in occlusal outline with only three persistent fossettes (anterolabial, posterolabial, posterolingual); P_4 with shallow lingual inflection and three persistent fossettids (anterior, lingual, posterior).

Etymology.—Greek, *tri-*, three; *lakkos* lake; *gaulus*, bucket (root for other mylagaulids).

Discussion.—Most of the differences between *Promylagaulus* and *Trilaccogaulus* occur in the morphology of P^4_4. In *Trilaccogaulus* only three enamel lakes are present in moderately worn specimens of P^4. *Promylagaulus* retains four fossettes on P^4 until the very latest stages of wear. P^4 of *Trilaccogaulus* lacks an anterolingual fossette in all specimens with at least moderate wear. The anterolabial fossette of *Trilaccogaulus* is expanded anteriorly and that of *Promylagaulus* is always narrow and anteroposteriorly elongate. In some specimens of *Promylagaulus* with little or no wear, there is a minute accessory fossette anterior to the anterolingual fossette. In some specimens, this fossette has united with the anterolabial fossette to form a bifurcated anterior end to the anterolabial fossette (a character also found in *Mesogaulus,* Black and Wood, 1956; Wilson, 1960). The ratio of buccolingual width of the anterolabial fossette of P^4 to the transverse width of the tooth (Fig. 11) ranges from 0.26 in *T. lemhiensis* to a maximum of 0.44 in *T. ovatus.* In specimens of *P. riggsi* (not including lingual bifurcation), this ratio is markedly lower, and ranges from 0.07 to 0.20.

Trilaccogaulus always maintains an oval P^4 even in late stages of wear. The P^4 of *Promylagaulus* is oval in occlusal outline in little worn and moderately worn

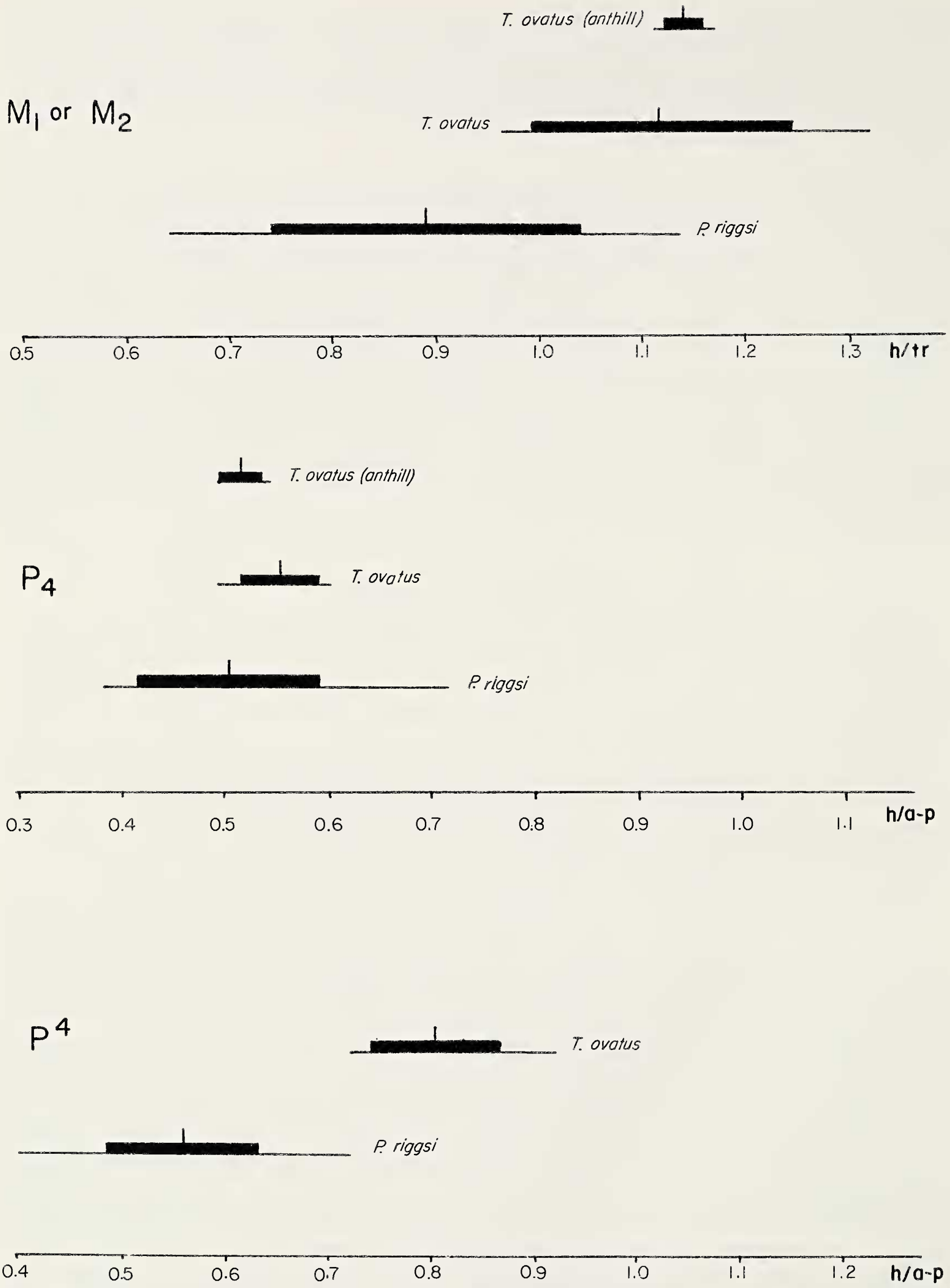


Fig. 10.—Comparison of crown height between *Trilaccogaulus ovatus* and *Promylagaulus riggsi* from McCann Canyon local fauna and topotypic material of *T. ovatus* from South Dakota. Horizontal lines represent total range, heavy bars represent one standard deviation, and vertical lines represent mean values. Data for *T. ovatus* from South Dakota anthills (LACM locality 1871) taken from Rensberger (1979). See text and Table 6 for abbreviations.

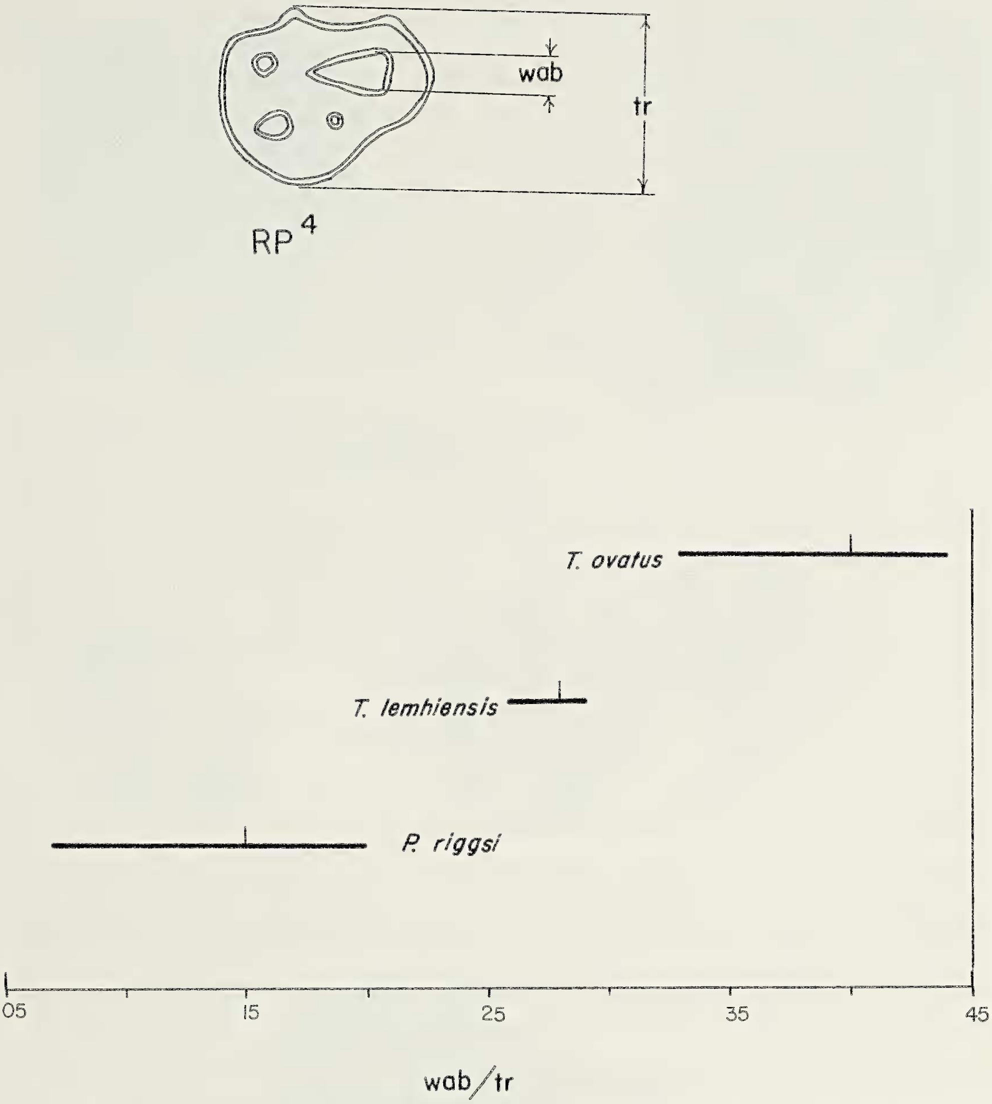


Fig. 11.—Ratio of anterior buccolingual width of the anterolabial fossette of P^4 versus the maximum transverse width of P^4 (wab/tr) in *Trilaccogaulus* and *Promylagaulus riggsi*. Horizontal bar represents range, vertical line demarks mean value.

specimens, but is more squared in very worn specimens such as the holotype. The angle of the wear facet on the anterocone of P^4 of *P. riggsi* was cited as a species character by Rensberger (1979). With a larger sample of *P. riggsi* available, it appears that this character is variable and should not be considered diagnostic.

P_4 of *Trilaccogaulus* differs from that of *Promylagaulus* in the possession of a lingual fossettid and lack of development of the posteriorlabial inflection. In *Promylagaulus* no lingual fossettid develops mainly due to the shortness of the metastylid crest, and the labial inflection is wider and has a well-pronounced posterior extension. The P_4 of *Trilaccogaulus,* like P^4, possesses three large fossettids on moderately and well-worn specimens. The posterior fossettid on P_4 of *Trilaccogaulus* is also larger and more persistent than that of *Promylagaulus.*

The lower molars of *P. riggsi* differ from those of *Trilaccogaulus* in the lack of a mesoconid or buccally directed spur from the mesoconid. In moderately worn specimens this can be determined by the anteroposterior length of the labial inflection. In *P. riggsi* it extends much farther posteriorly than in *Trilaccogaulus* where the mesoconid spur has fused with the hypoconid, in early stages of wear producing a minute fossettid, then resulting in a shallow labial inflection that does not extend posteriorly. There are no observable differences between *Promylagaulus* and *Trilaccogaulus* in the occlusal morphology of the upper molars, mandible, incisors or P^3.

No morphological differences could be found for isolated upper molars from Cr-117 and Cr-125 to separate *Promylagaulus* from *Trilaccogaulus* (Rensberger, 1979:12–13). If the range of crown height index is similar to that of the lower molars, the teeth with the highest crowns belong to *T. ovatus* and those with the lowest values belong to *P. riggsi.* However, if an equivalent 40% overlap occurs, determination of species is impossible. Only one maxilla with associated upper molar and P^4 (UNSM 81004) is present in the UNSM collections. The premolar is of *P. riggsi* morphology and crown height, and the M^1 has a crown height index (h/tr) of 0.93, which is in the middle of the range observed (0.61 to 1.32), most likely in the area of overlap between the two species.

Trilaccogaulus ovatus (Rensberger, 1979)
(Fig. 10F–J, Table 7)

Referred specimens.—From Cr-117 and Cr-125: UNSM 81017–81020, 81026, 24149–24152, P^4s; 81008, 81009, 24148, P_4s; 24142, eight isolated lower molars.

Discussion.—The distinctive characters of *Trilaccogaulus ovatus* were described by Rensberger (1979). Although the means of some of the crown height measurements of topotypic specimens of *T. ovatus* from South Dakota are slightly different from those of the Nebraska material (higher on lower molars, lower on P_4), all measurements of the South Dakota material are within the observed range of measurements of the referred specimens from Cr-117 and Cr-125 (Table 7).

Family Sciuridae Gray, 1821
Protosciurus Black, 1963
Protosciurus sp.
(Fig. 12A, B; Table 6)

Referred specimens.—UNSM 24018, RP^4; UNSM 24019, RM^1 or M^2; UNSM 24090, RM_3.

Locality.—UNSM locality Cr-125.

Description.—Small species of *Protosciurus* (Black, 1963:147; Table 6); P^4 smaller than M^1; parastyle buccolingually elongate, widely separated from paracone; protoloph running directly lingually from paracone to protocone; no indication of protoconule; mesostyle moderately large; metaconule large, circular; metaloph not continuous to protocone; posterior cingulum extending entire width of tooth.

Anterior cingulum extending entire width of M^1, widely separated from protoloph; no evidence of protoconule on protoloph; mesostylid relatively large; metaconule large, round; metaconule connected to protocone by weak loph.

M_3 with small anteroconid in place of anterior cingulum; trigonid open posteriorly, partially blocked by short posterior arm of protoconid; metaconid highest cusp; entoconid lingually placed; ectolophid

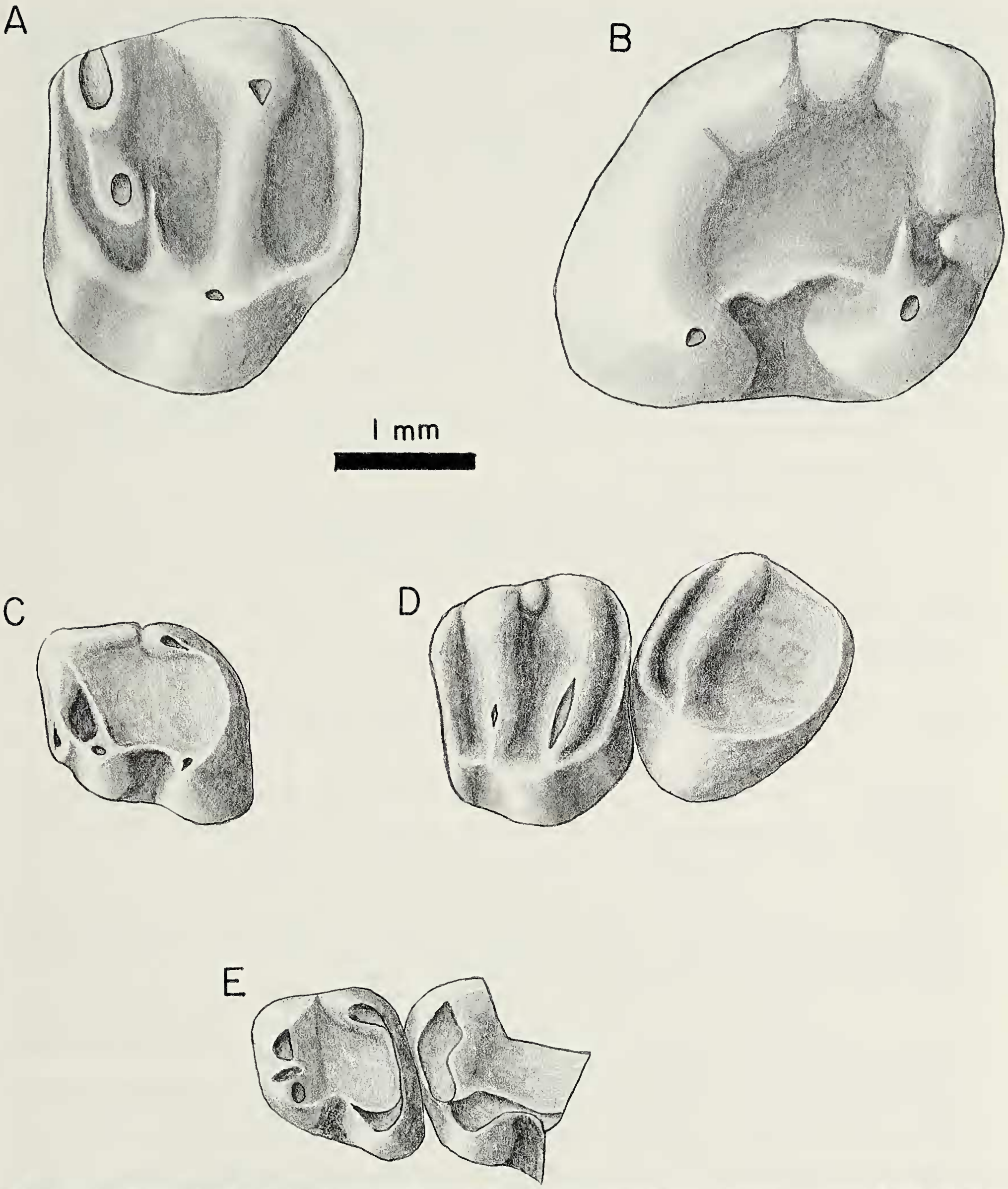


Fig. 12.—Sciurids from the Harrison Formation. A, B, *Protosciurus* sp. A, UNSM 24109, RM^1 or M^2. B, UNSM 24090, RM_3. C–E, *Nototamias quadratus*. C, UNSM 24103 (holotype), LM_1. D, UNSM 24106, LM^2–M^3. E, UNSM 24107, LP_4–M_1 (part).

narrow, weak loph; entoconid reduced to size of mesostylid; posterolophid running into series of three cuspules (including entoconid) at posterolingual corner of tooth.

Discussion.—Among the Arikareean species of *Protosciurus*, the McCann Canyon specimens most closely approach *P. rachelae* in size but are morphologically closer to *P. condoni* (both species are known from the John Day Formation, Oregon). The distinct, large metaconule on M^1 of the McCann Canyon material

(UNSM 24019) is present on upper molars of *P. condoni,* but in the latter is much larger than in the Nebraska specimens. Conversely, specimens of *P. rachelae* are nearly equal in size to the Nebraska specimens but the upper molars lack conules.

A single specimen from the Monroe Creek Formation, Wounded Knee area, South Dakota (SDSM 633) was referred by J. R. Macdonald (1970) to *Protosciurus* sp. This specimen is a partial maxilla with M^2–M^3. The cheek teeth of this specimen are much larger than those of the Nebraska specimens (near size of *P. condoni*) and lack conules. L. J. Macdonald (1972) referred several isolated teeth from the Monroe Creek Formation (anthill fauna) to "Sciurid, large species." These specimens agree in morphology with the Nebraska specimens of *Protosciurus* sp., but are slightly larger. It is likely that these South Dakota specimens are the same species as the Nebraska material. When a larger collection from Nebraska is known, the size ranges of these two populations may converge.

The Nebraska specimens clearly belong to a species of *Protosciurus* not previously described. At present the *Protosciurus* from Nebraska is too poorly represented to name a new species.

Nototamias Pratt and Morgan, 1989
Nototamias quadratus, new species
(Fig. 12C–E; Table 6)

Sciurid, small species L. Macdonald, 1972.

Holotype.—UNSM 24013, isolated LM_1 or M_2.

Referred specimens.—UNSM 24016, partial maxilla with LM^2–M^3; UNSM 24016, partial mandible with LP_4–M_1; UNSM 24014, RdP^4; UNSM 24106, LM_1 or M_2; UNSM 24106, RM_3.

Type locality.—UNSM locality Cr-117.

Diagnosis.—Conules lacking on protoloph and metaloph on upper molars; entoconid and mesostylid distinct and separate by narrow valley on lower molars; metalophulid I and metalophulid II continuous on M_1 and M_2.

Etymology.—Latin, *quadratus,* squared.

Description.—DP^4 small, triangular; parastyle large, widely separated from paracone; no protoconule on protoloph; mesostyle distinct, connecting to apex of paracone by short loph; hypocone crescentic, lingual to protocone; metaconule large and buccolingually elongate.

M^2 with parallel anterior and posterior margins; anterior and posterior cingula widely separated from proto- and metalophs; proto- and metalophs low, continuous lophs, connecting to anteroposteriorly-broadened, crescentic protocone; no conules present; mesostyle relatively large. M^3 as in M^2 but lacking metaloph and metacone, not expanded posteriorly.

Lower molars with squared posterolingual corner, trigonid slightly narrower buccolingually; anterior cingulum (metalophulid I) continuous with protoconid; anteroconid present only on holotype with weak groove separating protoconid (M_1); anteroconid and protoconid groove absent on M_2s; metalophulid II low, complete from protoconid to metaconid closing trigonid basin posteriorly; mesostylid distinct, round; mesoconid absent; entoconid continuous with posterolophid, distinct; narrow, deep valley separating entoconid and mesostylid; two roots present on all lower cheek teeth, both anterior and posterior roots buccolingually elongate.

M_3 elongate posteriorly; trigonid open posteriorly; entoconid indistinguishable part of posterolophid; narrow valley separating metaconid from anterior extension of posterolophid.

P_4 similar to molars but smaller; trigonid much narrower, closed anteriorly and posteriorly as in molars.

Discussion.—The lower molars of the small sciruid from the McCann Canyon fauna can be referred to *Nototamias* as diagnosed by Pratt and Morgan (1989:95) based on: 1) absence of a mesoconid; 2) presence of a distinct metastylid; 3) reduction of the anterolabial groove; and 4) having two roots on the lower molars. The upper molars are similarly referable to *Nototamias* because they lack a metaconule. No mandibles of *N. quadratus* are known so none of the characters of the mandible used to separate *Nototamias* from *Tamias* and *Eutamias* can be compared.

Black (1963) described *Tamias* sp. from the Sharps Formation, South Dakota. The specimens here referred to *Nototamias quadratus* differ from those specimens only in the enclosed trigonid on P_4. The dental feature of *N. quadratus* that separates it from all other Tertiary and Recent species of *Nototamias, Tamias* and *Eutamias* is the more distinct entoconid (reduced to part of a continuous posterolophid in all other species) that is more posteriorly positioned and separated from the mesostylid by a narrow valley. The complete metalophulid II in the lower cheek teeth of *N. quadratus* is present in Barstovian and Hemingfordian tamiines but not in those from the early Arikareean Sharps Formation.

L. J. Macdonald (1972) described several specimens of a small sciurid from an anthill collection of the Monroe Creek Formation, South Dakota. Those specimens agree in size and morphology with the Nebraska specimens of *N. quadratus* and should be referred to that species.

Pratt and Morgan (1989:fig. 2, node 4) considered the two-rooted lower molars of *Nototamias* as derived, and the four-rooted lower molars of *Eutamias* and *Tamias* as primitive. However, the number and shape of lower molar roots of *Nototamias* are similar to those of the earliest sciurids, and also those of the ischyromyids from which the sciurids were derived (Wood, 1962; Korth, 1984). Thus, it is more likely that the four-rooted condition of the lower molars is derived.

Family Castoridae Gray, 1821
Palaeocastor cf. *P. simplicidens* (Matthew, 1907)

Referred specimens.—FAM 64614, fragmentary mandible with RP_4–M_3; and UNSM 24154 to 24158, 85 isolated teeth.

Discussion.—The single specimen (FAM 64614) originally identified as *Palaeocastor fossor* by Skinner et al. (1977) was later referred to *Euhapsis barbouri* (Skinner and Johnson, 1984) based on identification by T. M. Stout. L. D. Martin (1987) erected a new genus, *Pseudopalaeocastor,* for *P. barbouri.* However, specimens from Cr-117 and Cr-125 do not appear to be referable to *P. barbouri* (*sensu* Martin, 1987). The single partial mandible with all of the cheek teeth present (FAM 64614) is too large to represent *P. barbouri* (total anteroposterior length of lower cheek tooth row 13.7 mm). P_4 is much more elongate in FAM 65614 than in figured specimens of *P. barbouri* (Stirton, 1935:fig. 39), and more nearly approaches the size and morphology of the lower premolar in *Palaeocastor simplicidens.*

Since cranial features rather than dental characters of the cheek teeth are diagnostic for palaeocastorine beavers (L. D. Martin, 1987), it is difficult to make a specific identification based on the material at hand (isolated cheek teeth only). Based on the size and shape of the incisors available, the material most likely represents *Palaeocastor simplicidens.*

Family Heteromidae Gray, 1868
Subfamily ?Heteromyinae Gray, 1868
Hitonkala Macdonald, 1963

Type species.—*H. andersontau* Macdonald, 1963.

Range.—Arikareean (late Oligocene to early Miocene) of South Dakota and Nebraska.

Emended diagnosis.—Small heteromyid, near size of most species of *Proheteromys*; P_4 highly molariform with three major cusps on metaloph (metaconid, protoconid, parastylid); anterior cingulum on upper molars running entire width of tooth and continuous across lingual length of tooth on M^2–M^3 with stylar cusps reduced or absent; lingual cingulum on M^1 cut by narrow valley between protostylid and hypostylid.

Discussion.—The molariform P_4 of *Hitonkala* is seen elsewhere among the heteromyids only in the later Tertiary *Oregonomys* J. E. Martin (1984) and Recent *Heteromys* and *Liomys* (Wood, 1935). *Hitonkala* is separable from these genera by the lower crown height of the cheek teeth and the morphology of the lingual cingulum on the upper molars. Contemporaneous species of *Proheteromys* lack the molarization of P_4 as well as the configuration of the anterior and lingual cingula on the upper molars. In all species of *Proheteromys* the lingual cingulum on the upper molars (at least M^1 and M^2) is interrupted by a narrow valley at its center, and two stylar cusps are present. In *Hitonkala,* the cingulum is continuous and lacks styles on M^2 and M^3.

It is difficult to assign *Hitonkala* to a known subfamily of the Heteromyidae. The morphology of P_4 most closely resembles that of heteromyines (Wood, 1935) but the cranial criteria used for separating the subfamilies of heteromyids (Wahlert, 1985) have not been determined for *Hitonkala.* Two partial skulls of *H. andersontau* (J. R. Macdonald, 1963, 1970) are currently known, which should provide enough data to determine the subfamilial rank of *Hitonkala.*

Hitonkala macdonaldtau, new species
(Fig. 13B–D; Table 8)

Holotype.—UNSM 24024, maxilla with LP^4–M^2.

Referred specimens.—UNSM 24025, 24027, 24029, 24031, 24032, 24033, 24034, 24035, partial maxillae with upper cheek teeth; UNSM 24036, 24103, mandibles with cheek teeth; UNSM 24037, mandible with I_1; UNSM 24023, 24038, isolated cheek teeth.

Type locality.—UNSM locality Cr-117.

Diagnosis.—Slightly larger than *H. andersontau* (J. R. Macdonald, 1963:table 10; Table 8); accessory cusps on protoloph of P^4; P_4 with lower, more posterior protoconid.

Etymology.—Patronym for J. R. Macdonald; *tau,* Sioux possessive ending.

Description.—Mandible shallow; masseteric scar typical for heteromyid (see Wood, 1935); diastema long, shallow; I_1 laterally compressed, convex anteriorly, flattened medially and laterally; enamel extending slightly higher on lateral side of tooth than on medial.

P_4 with protostyle and metaconid subequal; anteroconid small, distinct, anterior to metaconid and protostyle; protocone low swelling posterior to other metalophid cusps; narrow ridge extending posteriorly from metaconid on UNSM 24036, along lingual side of low protoconid; hypolophid consisting of hypoconid and entoconid, no hypostylid; small hypoconulid on UNSM 24036; hypolophid wider than metalophid.

M_1 and M_2 nearly identical; M_2 slightly smaller; stylar cusps distinct, making tooth bilophate (three cusps each loph); anterior cingulum extending from center of anterior margin of protoconid around anterobuccal corner of tooth, ending posteriorly at protostyle, slightly posterior to protoconid; posterior cingulum variably present on M_1; absent on M_2.

M_3 metalophid as in anterior molars; hypolophid lacking hypostylid; M_3 smaller than anterior molars.

P^4 largest upper cheek tooth; protoloph dominated by large, circular protocone; accessory cusps present on all unworn specimens except UNSM 24034 which has buccolingually elongate protocone; two specimens with both paracone and protostyle, three specimens with paracone only, one specimen with protostyle only (all others worn); metaloph three-cusped; hypostyle and metacone subequal in size; hypostyle not extending anterior to hypocone.

Table 8.—*Dental measurements of heteromyid rodents from Cr-117 and Cr-125. Measurements in mm.*

	P^4		M^1		M^2		
UNSM no.	a-p	tr	a-p	tr	a-p	tr	
Hitonkala macdonaldtau							
24023	1.45	1.66					
24023	1.66	1.79					
24024	1.72	1.76	1.25	1.71	1.15	1.54	(type)
24025	1.52	1.65					
24027			1.39	1.82	1.27	1.69	
24029	1.48	1.70					
24031	1.44	1.61	1.14	1.55			
24032	1.68	1.64	1.25	1.60			
24033	1.43	1.72					
24034	1.50	1.76					
24035	1.59	1.66					
Proheteromys sp.							
24026	1.34	1.60					
24028	1.30	1.59	1.11	1.41			
24030	1.25	1.53	1.12	1.51			

	P_4			M_1			M_2			M_3		
	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp
Hitonkala macdonaldtau												
24036	1.20	0.88	1.10	1.38	1.41	1.41						
24103	1.14	0.98	1.08	1.31	1.29	1.35	1.29	1.41	1.33	1.25	1.27	1.10

M^1 largest molar; both protoloph and metaloph three-cusped; stylar cusps nearly equal to major cusps in size; lingual cingulum broken at central transverse valley between lophs; anterior cingulum originating at anterior margin of paracone, running continuously around anterolingual corner of tooth, terminating posteriorly at protostyle; no posterior cingulum.

M^2 similar to M^1 except lingual cingulum continuous, blocking central transverse valley lingually; stylar cusps present but low.

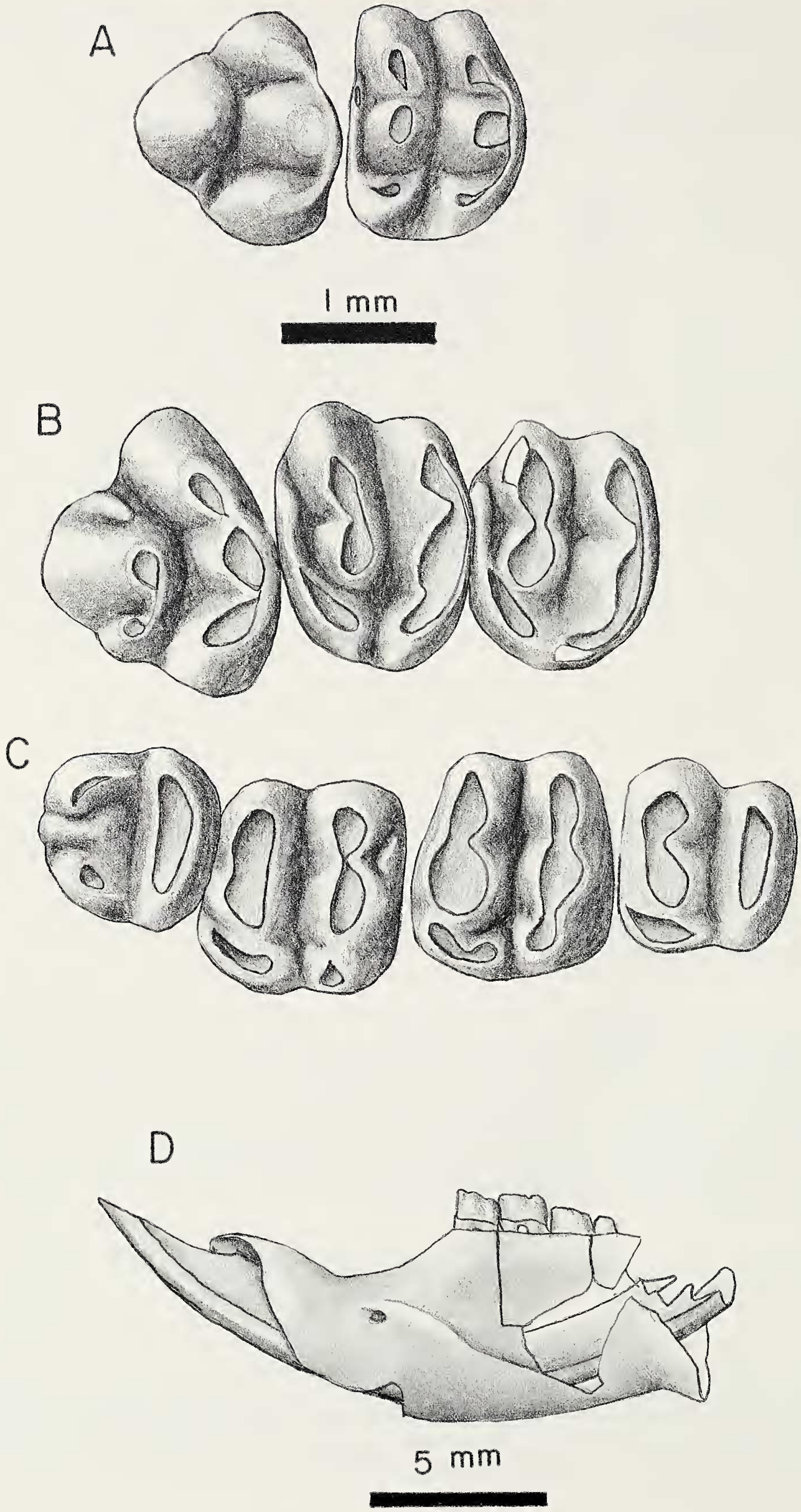
M^3 not preserved but alveolus present in holotype; smaller than M^2.

Discussion.—The morphology of P_4 (three-cusped metalophid) and the upper molars (broken lingual cingulum on M^1, continuous on M^2) makes this species clearly referable to *Hitonkala. Hitonkala macdonaldtau* differs from *H. andersontau* in its larger size, the presence of accessory cusps on the protoloph of P^4, and the lower, smaller protoconid on P_4. The size and greater complexity of P^4 of *H. macdonaldtau* are derived conditions compared to the older *H. andersontau* from the early Arikareean Sharps Formation.

Proheteromys Wood, 1932
Proheteromys sp.
(Fig. 13A; Table 8)

Referred specimens.—UNSM 24026, 24028, and 24030, partial maxillae with cheek teeth.

Discussion.—The three maxillae referred here to *Proheteromys* sp. differ from the material referred above to *H. macdonaldtau* in being smaller and having no accessory cusps on the protocone of P^4.


A
1 mm
B
C
D
5 mm

Currently, the systematics of *Proheteromys* is confused. Twelve species referred to this genus range in age from Orellan (Galbreath, 1953) to Barstovian (James, 1963). Geographically, the species of *Proheteromys* range from Florida (Wood, 1932) to California (James, 1963) and Saskatchewan (Skwara, 1988). J. R. Macdonald (1963, 1970) recognized four species from the Arikareean of South Dakota; *P. fedti, P. gremmelsi,* and *P. bumpi* from the Sharps Formation, and *P. ironcloudi* from the overlying Monroe Creek Formation. It is also possible that *P. parvus* (Troxell, 1923) may represent an Arikareean species from Colorado (see Wood, 1935:171 for discussion of age). J. R. Macdonald (1970) questioned whether all three species recognized from the Sharps Formation were real or individual variants of one species. Due to the small sample size, he was unable to define the range of morphological variation and consequently maintained all three species as distinct.

L. D. Martin (1973), on the basis of a single specimen from the Gering Formation of Nebraska, suggested that the Sharps "species" should be included under *P. fedti.* However, if measurements of all the known specimens from the Sharps are combined (J. R. Macdonald, 1970:tables 24, 25, 26), the coefficients of variation are high (some over ten), which makes it unlikely that only one species is represented. It appears most likely, based on dental measurements, that *P. gremmelsi* and *P. bumpi* may be conspecific. Specimens referred to *P. fedti* are significantly smaller than those of *P. gremmelsi* and *P. bumpi,* and may represent a distinct species.

Proheteromys parvus has dental measurements very near those of *P. fedti* (Wood, 1935:table II), and has only a minor variation of P_4 (lack of minute anteroconid). It is possible that *P. fedti* and *P. parvus* are synonymous.

All of the specimens from Cr-117 and Cr-125 are maxillae with upper cheek teeth. As none of the described Arikareean species of *Proheteromys* are currently known from upper cheek teeth, no direct comparison can be made. However, in size (Table 8) the Nebraska specimens most closely match specimens of *P. fedti.*

Family Florentiamyidae Wood, 1936*a*
Sanctimus Macdonald, 1970
Sanctimus cf. *S. stuartae* Macdonald, 1970
(Fig. 14G–L; Table 9)

Referred specimens.—UNSM 24095 and 24096, isolated P^4s; UNSM 24100, RP_4; UNSM 24099, LdP_4; UNSM 24097, isolated upper molar; UNSM 24101, four isolated upper molars; UNSM 24102, seven isolated lower molars; UNSM 24098, LM_3.

Description.—P^4 (UNSM 24095) as described for *S. stuartae* and *S. stouti* (J. R. Macdonald, 1970; Wahlert, 1983), valley between hypostyle and entostyle deeper; UNSM 24096 lacking protostyle.

Both lower and upper molars typical for florentiamyid; anterior cingulid present on half of referred lower molars; intermediate in size between *S. stuartae* (J. R. Macdonald, 1970:table 28) and *S. stouti* (Wahlert, 1983:tables 2, 3; Table 9).

P_4 with single, anteroposteriorly elongate protostylid, subequal to metaconid in size; protoconid small, central, slightly closer to metaconid than protostylid; hypoconid and entoconid large, equal in size; hypostylid small; minute cuspule in central transverse valley anterior to hypoconid; minute hypoconulid present.

←

Fig. 13.—Heteromyid rodents from the Harrison Formation. A, *Proheteromys* sp., UNSM 24030, LP^4–M^1. B–D, *Hitonkala macdonaldtau.* B, UNSM 24024 (holotype), LP^4–M^2. C, UNSM 24103, LP_4–M_3. D, UNSM 24103, lateral view of mandible.

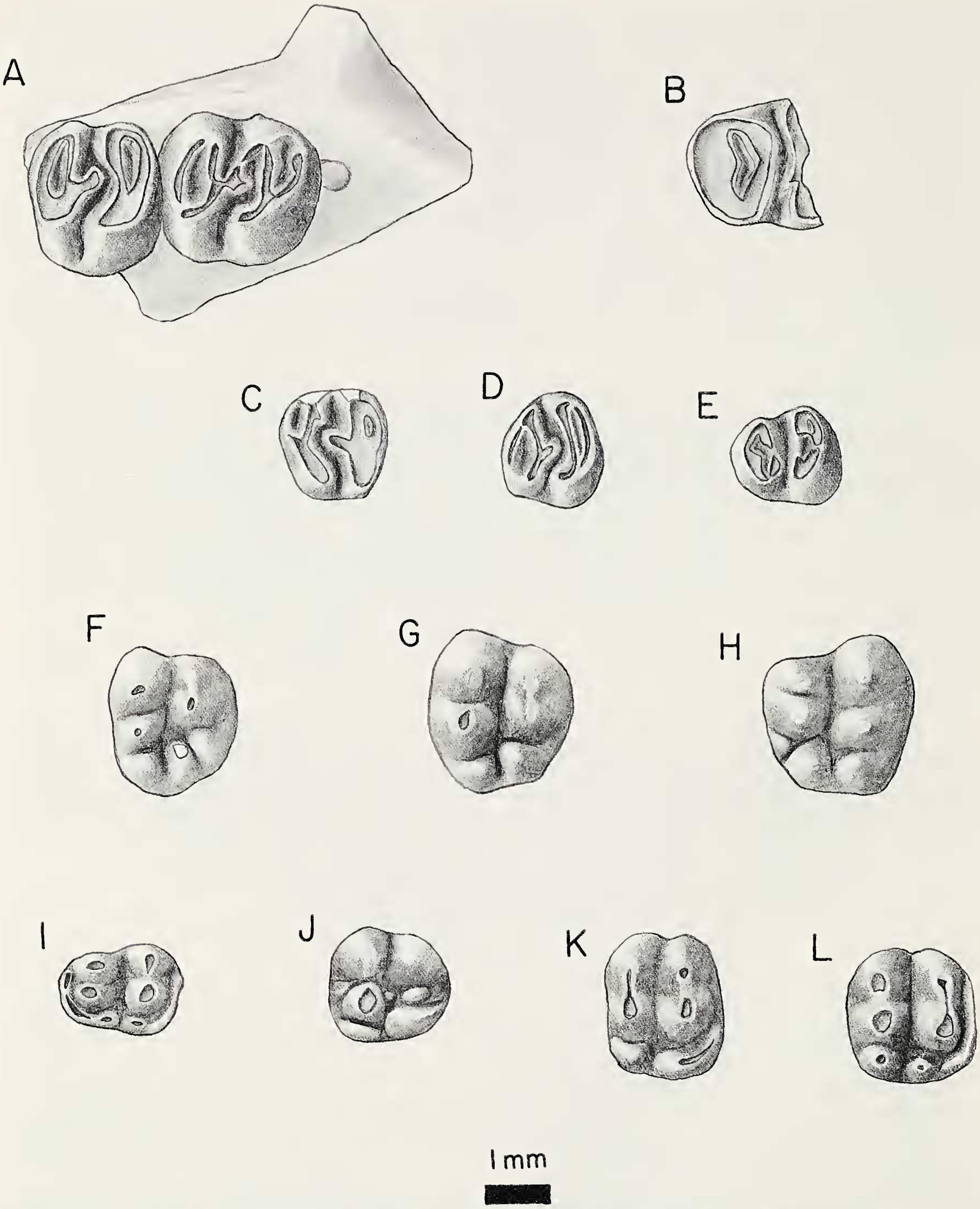


Fig. 14.—Eomyids and florentiamyids from the Harrison Formation, Nebraska. A, B, *Arikareeomys skinneri.* A, UNSM 81031 (holotype), partial maxilla with LP^4–M^1. B, UNSM 24153, LP$_4$ (part). C–E, *Pseudotheridomys* sp. C, UNSM 81091, LP^4. D, UNSM 24104, RM^3. E, UNSM 81032, LP$_4$. F, *Florentiamys* sp., UNSM 24094, RP^4. G–L, *Sanctimus* cf. *S. stuartae.* G, UNSM 24096, RP^4. H, UNSM 24095, LP^4. I, UNSM 24099, LdP$_4$. J, UNSM 24100, RP$_4$. K, UNSM 24102, RM$_1$ or M$_2$. L, UNSM 24102, RM$_1$ or M$_2$.

Table 9.—*Dental measurements of* Sanctimus *cf.* S. stuartae *from Cr-117 and Cr-125. Measurements in mm.*

	P^4			M^1 or M^2		P_4			M_1 or M_2		
UNSM no.	a-p	tra	trp	a-p	tr	a-p	tra	trp	a-p	tra	trp
							1.25				
							1.64				
24095	2.10	2.16	2.41								
24096	2.28	1.95	2.43								
24097				1.98	2.47						
24101				1.78	2.36						
24101				1.91	2.50						
24101				1.83	2.39						
24101				1.86	2.57						
24099						1.87	1.42 (d)				
24100						1.93	1.80				
24102								1.83	2.16	1.98	
24102								1.76	2.06	1.96	
24102								1.91	1.96	1.97	
24102								1.82	2.30	2.20	
24102								1.83	2.20	2.08	
24102								1.86	2.16	2.12	
24102								1.86	2.12	1.96	

DP_4 smaller than P_4; anteroposteriorly elongate; major cusps (protoconid, metaconid, hypoconid, entoconid) equal in size; stylar cusps small; anterior cingulid convex anteriorly running from anterior margin of metaconid to protostylid; protoconid isolated in trigonid basin; minute hypoconulid present.

Discussion.—The only major difference between *Sanctimus stuartae* from the Sharps Formation in South Dakota (J. R. Macdonald, 1970) and *S. stouti* from the Monroe Creek Formation in Wyoming (Wahlert, 1983) is size. *Sanctimus stouti* is slightly larger. The UNSM material from the McCann Canyon fauna is intermediate in size between these two species. The only dental feature used to separate these species is the presence of a hypostylid on P_4 of *S. stouti,* and its absence on specimens of *S. stuartae.* But this cusp on UNSM 24100 from Cr-117 and the type of *S. stouti* is minute and suggests variation within a single species. Hence, it seems more appropriate to recognize a single species of *Sanctimus* with a slight size increase over time.

The lack of a protostyle on one P^4 (UNSM 24096) is a condition unknown in species of *Sanctimus.* However, it does occur in a single species of *Florentiamys.* Wahlert (1983) named *Florentiamys kennethi* (based on the holotype only), which also lacked this cusp, arguing that the protostyle had fused with the entostyle. Because UNSM 24096 is identical in all other features with another P^4 from Cr-117 (UNSM 24095) which has a protostyle, it is believed that they both represent the same species and that the lack of a protostyle is variable and not a distinction between species. Since most species of *Florentiamys* and *Sanctimus* are known from one or only a few specimens, the full extent of character variation is not fully understood.

The variable presence of an anterior cingulid on the lower molars of *Sanctimus* from the McCann Canyon fauna also suggests that another synonymy among florentiamyids is possible. The only difference cited by Wahlert (1983) between *Florentiamys loomisi* and *F. kingi* is the anterior cingulid on the lower molars. On the holotype and only specimen of *F. kingi,* the lower molars are worn and no evidence of an anterior cingulid can be detected. Therefore, it is quite likely that *F. kingi* is a junior synonym of the type species of the genus, *F. loomisi.*

Florentiamys Wood, 1936*a*
Florentiamys sp.
(Fig. 14F)

Referred specimen.—UNSM 24094, RP^4.

Locality.—UNSM locality Cr-117.

Discussion.—UNSM 24094 is smaller than the upper premolars referred above to *Sanctimus,* has a protostyle more closely appressed to the entostyle as in *Florentiamys*; in *Sanctimus* the protostyle is closer to the protocone. UNSM 24094 is smaller than any previously described specimen of *Florentiamys* (a-p, 1.89 mm; tra, 1.80 mm; trp, 2.15 mm; also see Wahlert, 1983:table 2), and differs from all known species of *Florentiamys* in the size of the stylar cusps. Typically in *Florentiamys* the stylar cusps are small and the valleys that separate them are shallow and disappear with moderate wear. The stylar cusps of UNSM 24094 are nearly as large as the major cusps, and, though closely appressed, are separated by deep valleys.

The difference between UNSM 24094 and the premolars referred above to *Sanctimus* is far greater than can be explained by individual variation. The size of the stylar cusps is unique among species of *Florentiamys.* UNSM 24094 apparently represents a distinct species of *Florentiamys.*

Family Geomyidae Bonaparte, 1845
Subfamily Entoptychinae Miller and Gidley, 1918
Entoptychus Cope, 1878
Entoptychus grandiplanus, new species
(Fig. 15; Table 10)

Holotype.—UNSM 24039, mandible with RI_1, P_4–M_3.

Referred specimens.—UNSM 24041–24055 and 24079–24086, mandibles with lower cheek teeth; UNSM 24057, ten isolated P_4s; UNSM 24056, 17 isolated upper incisors; UNSM 24058–24064 UNSM 24066, 24067 and 24069–24073, maxillae with upper cheek teeth; UNSM 24074, fused frontal bones; UNSM 24075, palate without cheek teeth; UNSM 24076, 60+ isolated cheek teeth; UNSM 24077, 300+ isolated cheek teeth; UNSM 24068, dP_4; and UNSM 24093, dP^4.

Type locality.—UNSM locality Cr-117.

Diagnosis.—Smallest species of the genus; no enamel failure or dentine chevrons on cheek teeth (low crowned); metaconid (and sometimes protostylid) of P_4 elongate, oriented posteriorly toward center of tooth; diastema of mandible shorter than in Oregon species.

Etymology.—Latin, *grandis,* great; *planus,* plain.

Description.—Mandible relatively deep; diastema long, shallow; mean ratio of length of diastema to occlusal length of lower cheek tooth row 1.08; wide area of articulation for symphysis, dorsally extending about one-third length of diastema, ventrally small chin process present below anterior root of P_4; mental foramen small, at mid-depth of mandible below posterior half of diastema; masseteric

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Fig. 15.—Dentition of *Entoptychus grandiplanus.* A, UNSM 24093, LdP^4. B, C, UNSM 24059, RP^4–M^3. B, Occlusal view. C, Buccal view. D, UNSM 24068, LdP_4. E, UNSM 24057, LP_4. F, UNSM 24057, RP_4. G, H, UNSM 24039 (holotype). G, RP_4–M_3. H, Lateral view of mandible.

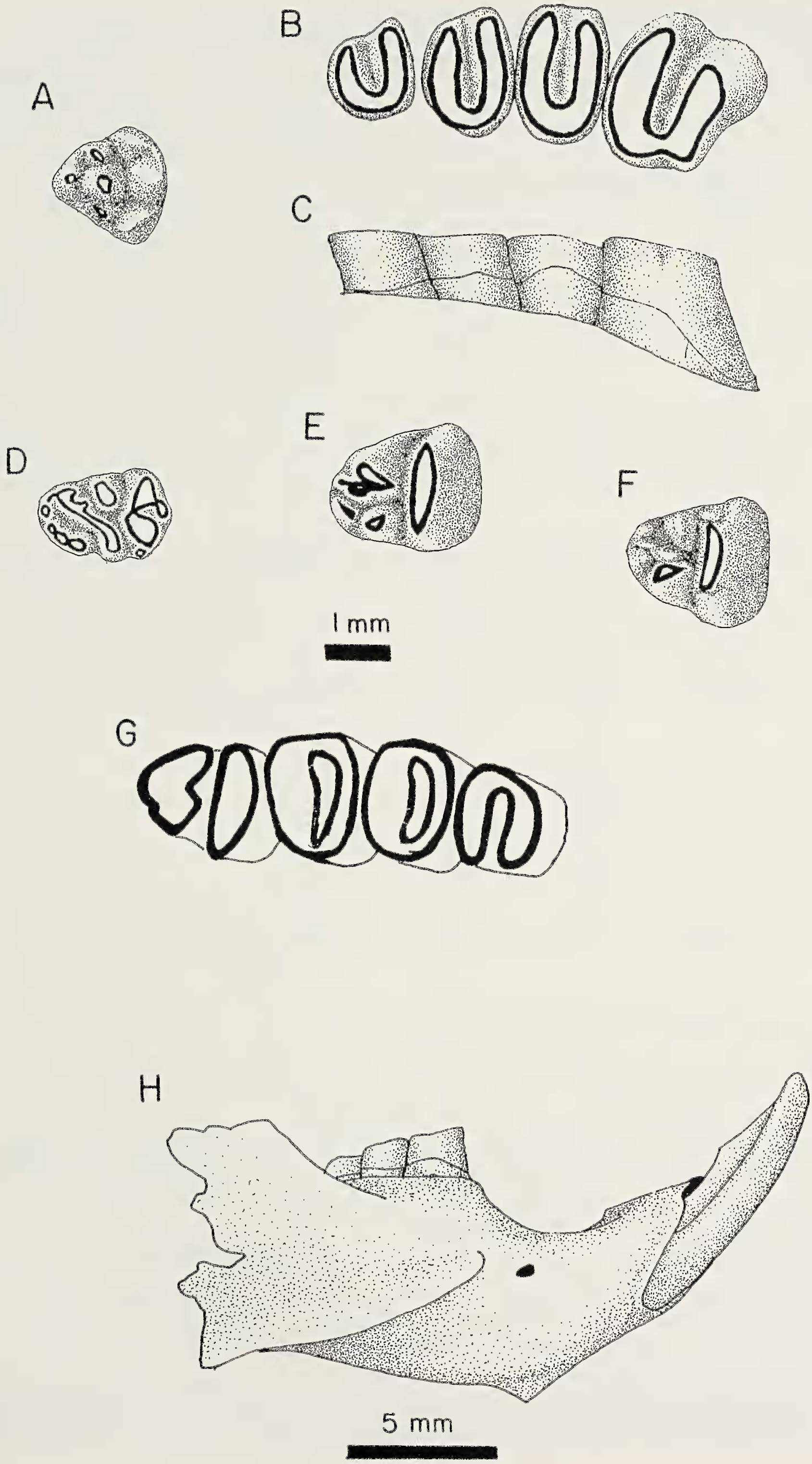

A
B
C
D
E
F
1 mm
G
H
5 mm

Table 10.—*Dental measurements of* Entoptychus grandiplanus. *Statistical abbreviations as in Table 7. Measurements in mm.*

		N	M	OR	S	CV
I^1	a-p	16	1.69	1.40–2.05	.16	9.9
	tr	16	2.16	1.80–2.55	.22	10.3
dP^4	a-p	1	1.75	—	—	—
	tra	1	0.95	—	—	—
	trp	1	1.88	—	—	—
P^4	a-p	20	2.34	2.05–2.78	.18	7.7
	tra	20	1.68	1.37–1.97	.13	7.8
	trp	20	2.08	1.82–2.32	.16	7.6
M^1	a-p	11	1.41	1.29–1.49	.06	4.0
	tr	11	2.08	1.85–2.18	.10	5.0
M^2	a-p	11	1.35	1.15–1.45	.09	6.8
	tr	11	1.95	1.85–2.09	.07	3.8
M^3	a-p	6	1.32	1.17–1.39	.08	5.8
	tr	6	1.56	1.48–1.65	.06	4.1
P^4–M^3		3	6.66	6.41–7.00	—	—
I$_1$	a-p	6	1.83	1.40–2.33	.30	16.0
	tra	6	1.52	1.26–1.87	.21	14.0
dP$_4$	a-p	1	1.97	—	—	—
	tra	1	1.09	—	—	—
	trp	1	1.32	—	—	—
P$_4$	a-p	30	1.82	1.52–2.17	.16	8.7
	a-p	29	1.41	1.12–1.60	.15	10.4
	trp	30	1.84	1.52–2.20	.14	7.5
M$_1$	a-p	18	1.48	1.34–1.58	.08	5.1
	tra	18	1.93	1.73–2.27	.14	7.1
	trp	18	2.00	1.81–2.33	.15	7.7
M$_2$	a-p	12	1.45	1.25–1.70	.11	7.9
	tra	12	1.93	1.75–2.20	.15	7.7
	trp	12	1.95	1.66–2.21	.16	8.2
M$_3$	a-p	6	1.42	1.18–1.59	.13	9.3
	tra	6	1.48	1.35–1.55	.07	4.8
P$_4$–M$_3$		5	6.30	5.99–6.80	.03	4.7
Length of lower diastema		11	6.29	4.70–7.55	.88	14.0

scar represented ventrally by heavy ridge running from angle to just posterior to mental foramen, then running directly dorsad and abruptly disappearing; ascending ramus rises laterally even with posterior margin of M$_2$; deep valley separating ascending ramus from tooth row; condyle well dorsad to tooth row; lateral expansion for base of incisor elongate, separated from ascending ramus by pronounced shelf; angular and coronoid processes not known.

I$_1$ triangular in cross-section; flat enamel face anteriorly; enamel extending only slightly onto lateral and medial sides.

DP$_4$ elongate, smaller than other cheek teeth; hypoconid and entoconid united, separated from metalophid by valley; loph arising from protostyle running obliquely across tooth to anterior cingulid; metaconid close to protostylid loph but not connecting; anterior cingulid anteriorly expanded as loph of small cuspules with shallow central valley.

P$_4$ metalophid three-cusped (metaconid, protoconid, protostylid); protoconid smallest cusp, anteriorly situated; anterior cingulid arising from center of protoconid, varying from small loph on anterior face of protoconid to series of small cuspules extending both lingually and buccally; anterior cingulid never joins metaconid or protostylid until late wear; metaconid equal to or larger than protostylid, elongate with posterior extension directed toward center of hypolophid; protostylid with similar posterior extension on some specimens, otherwise smaller than metaconid and oval in outline; hypolophid straight to gently concave anteriorly; hypostylid only recognizable cusp on unworn teeth; metalophid and hypolophid unite lingually with wear.

Lower molars show no evidence of enamel failure on lateral sides; molars decrease in size from M_1 to M_3; metalophid consisting of two subequal cusps (metaconid, protoconid) that unite anteriorly in a shallow "V"; protostylid minute, posterior to protoconid; anterior cingulid extending anteriorly from protostylid, wrapping around anterobuccal corner of tooth; anterior cingulid extending variably from one-half to entire width of tooth; hypolophid straight row of anteroposteriorly compressed cusps; both lophs wear to straight buccolingually oriented lophs; lophs unite buccally first, then lingually at very late stage of wear.

The only bones of the skull known for *E. grandiplanus* are the palate (maxillae) and frontals. Paired parasagittal crests on frontals, rising 0.54 mm above center; crests constrict slightly at postorbital constriction, then flare posteriorly; palate broad, distinct groove on either side of centerline; tooth rows slightly divergent posteriorly; palatine bones extending anteriorly to level even with center of M_1.

DP^4 smaller than P^4; anterocone buccolingually elongate, uniting with protocone by thin loph; protoloph anteriorly concave, three-cusped; protocone largest cusp on protoloph; metaloph wider than protoloph; hypocone largest cusp, uniting with other metaloph cusps by thin posterior cingulum; hypostyle transversely compressed, slightly anterior of hypocone, blocking transverse valley between lophs.

P^4 largest tooth; protoloph three-cusped, protocone largest cusp; protostyle anterior and lingual to protocone, distinct in later wear as anterolingual bulge in wear fosset; metaloph wider than protoloph, three-cusped; hypostyle smallest cusp, anterior to remainder of metaloph; metaloph wears to straight or slightly anteriorly convex loph; lophs unite lingually with wear.

Upper molars decrease in size from M^1 to M^3; unworn molars with two rows of three cusps, protostyle and hypostyle smallest; anterior cingulum extending from paracone to protostyle, leaving narrow valley between it and protocone; no posterior cingulum present; M^1 and M^2 wear to two parallel lophs, uniting lingually first, then buccally at late stage of wear; M^3 smallest tooth, nearly circular in outline; metaloph narrower (buccolingually) than protoloph.

Discussion.—Entoptychus grandiplanus is separable from *Gregorymys* based on the occlusal pattern of P_4 and dP_4 as defined by Rensberger (1971). *Entoptychus grandiplanus* differs from the Oregon species of *Entoptychus* only by its lower-crowned cheek teeth, lack of enamel failure on the lateral sides of the cheek teeth, smaller size, and relatively shorter diastema on the mandible. The lowest height of the crown on P_4 (RD of Rensberger, 1971:fig. 2) of the Oregon species is 1.55 mm. In *E. grandiplanus* this dimension is considerably less ranging from 0.83 to 1.35 mm (mean = 1.13 mm).

The three known species of *Entoptychus* from Montana and Idaho show similar lack of enamel failure as in *E. grandiplanus.* The only species from Montana with any loss of enamel is *E. montanensis* (Hibbard and Keenmon, 1950), which has the same development as the most primitive Oregon species (Rensberger, 1971: 77). The other two species recognized from Montana, *E. fieldsi* and *E. sheppardi* are larger than *E. grandiplanus* (Nichols, 1976:tables 4, 5, 6) and the metaconid and protostylid of P_4 are elongate and oriented posteriorly in a straight anteroposterior direction. In *E. grandiplanus* these cusps are convergent toward the center of the hypolophid. The manidibular diastema of *E. sheppardi* has a diastema length/tooth row length ratio of 0.93 (not known for *E. fieldsi*), lower than in *E. grandiplanus* which has a ratio of 1.08. In a measured sample of *Entoptychus* from the John Day Formation, this ratio ranges from 1.29 to 1.58 (mean = 1.43), much longer than either *E. grandiplanus* or *E. sheppardi.*

Progressive hypsodonty of the cheek teeth is characteristic of the genus *Entoptychus.* Its absence in Montana and Idaho species referred to this genus led McKenna (1980) to suggest that they, along with the specimens from Darton's Bluff

(Big Horn Mountains [McKenna and Love, 1972]) may represent a different genus. McKenna (1980) stressed the transitional morphology of these species between *Entoptychus* and *Gregorymys.* However, these species lack only the hypsodonty of the Oregon species of the genus and have a slightly shorter diastema. Thus, *E. fieldsi* and *E. sheppardi* show no similarity to *Gregorymys* other than in the crown height of the cheek teeth.

The specimens from Darton's Bluff referred to *Entoptychus* sp. (McKenna and Love, 1972) and later "Entoptychine geomyid" (McKenna, 1980) show increased hypsodonty and enamel failure on the cheek teeth, as in *Entoptychus* from Oregon, but have a much shorter diastema and different P_4 occlusal morphology. These features are shared with *Gregorymys kayi* Wood (1950), also from Montana. Rensberger (1971:footnote p. 17) noted that *G. kayi* is very *Entoptychus*-like in cheek tooth morphology, but retained it in *Gregorymys* because of its shorter diastema. It is likely that *E. grandiplanus* and the Montana species are correctly referred to *Entoptychus,* and the Darton's Bluff specimens are referable to a distinct genus which also contains "*G.*" *kayi.*

J. R. Macdonald (1970) identified a single specimen (LACM 9272) from the Sharps fauna as *Entoptychus minor.* This specimen is worn, so little can be told of the occlusal pattern of P_4, but it is equivalent in size to *E. grandiplanus* and lacks the degree of enamel failure on the cheek teeth of *E. minor.* Therefore, it may represent an even stratigraphically older specimen of *E. grandiplanus.*

Nichols (1976) noted that a skull from the Monroe Creek Formation (SDSM 6257) identified by J. R. Macdonald (1970) as *Gregorymys formosus* was similar to that of *E. sheppardi* with similar crown height of the cheek teeth. He did not refer this specimen to the Montana species because of differences in the morphology of P_4. According to Nichols' (1976:25) description of the premolar of the Monroe Creek specimen, it is very similar to P_4s of *E. grandiplanus.* The specimen, however, is too large to belong to the latter species, and may represent yet another low-crowned eastern species of *Entoptychus.*

Gregorymys Wood, 1936*b*

Gregorymys cf. *G. formosus* (Matthew, 1907)

Referred specimens.—UNSM 24040, mandible with LP_4–M_1; UNSM 24065, maxilla with RP^4–M^1; UNSM 24092, LI^1.

Locality.—UNSM locality Cr-117.

Description and discussion.—The three specimens referred here to *Gregorymys* are easily distinguishable from specimens of *Entoptychus grandiplanus* by their larger size. The upper incisor (UNSM 24092) is not only larger than any of *E. grandiplanus* (a-p, 2.4 mm; tra, 2.8 mm) but the entire anterior surface is convex. As noted by Rensberger (1971), the convexity of the anterior surface of upper incisors of *Entoptychus* begins at the center of the anterior surface and continues laterally. There is also a faint central groove on UNSM 24092 along with a deeper groove along the medial surface of the tooth. No recorded species of *Gregorymys* has both of these grooves on I^1. *Gregorymys riggsi* has only a central groove on I^1, and all other species (where known) have only a medial groove.

All of the cheek teeth in the referred specimens are heavily worn, so little can be told of the occlusal morphology. As in the cheek teeth of *E. grandiplanus,* there is no sign of enamel failure on any of these teeth. The estimated ratio of the mandibular diastema length to the tooth row length is only 0.93, lower than in any specimen of *E. grandiplanus* (see above discussion).

Table 11.—*Dental measurements of eomyid rodents from the Harrison Formation, Nebraska. Measurements in mm.*

	P^4		M^1		M^3		P_4		
UNSM no.	a-p	tr	a-p	tr	a-p	tr	a-p	tra	trp
Arikareeomys skinneri									
81031	2.28	2.05	1.90	2.13					
24153							–	1.92	2.22
Pseudotheridomys sp.									
81091	1.50	1.50							
24104					1.53	1.75			
81023							1.71	1.26	1.49

Family Eomyidae Depéret and Douxami, 1902
?Subfamily Yoderimyinae Wood, 1955
Arikareeomys, new genus

Type and only species.—*Arikareeomys skinneri*, n. sp.

Range.—Late Arikareean (earliest Miocene) of Nebraska.

Diagnosis.—Intermediate-sized eomyid; P^3 not present; P^4 longer than wide, and larger than M^1; cheek teeth mesodont and lophate; protoloph not connected to metaloph on upper cheek teeth; no mesoloph on upper molars; anterior and posterior cingula on M^1 and posterior cingulum on P^4 connected to paracone or metacone buccally, isolating enamel lakes; anterior cingulum widely separated from protoloph on P^4; anterior cingulid and metalophid of P_4 joining at buccal and lingual ends forming D-shaped enamel lake.

Etymology.—Named for the provincial age from which the type species came and the familial affinities of this genus.

Discussion.—*Arikareeomys* has higher-crowned cheek teeth than any other North American eomyid. It is approximately the same size as *Yoderimys* Wood (1955), smaller than the Hemphillian eomyids (Wood, 1936*c*; Jacobs, 1977; Dalquest, 1983), and larger than all other species of eomyids. The lack of a connection between the protoloph and metaloph of the upper cheek teeth is seen elsewhere only in *Pseudotheridomys hesperus* Wilson (1960) and the European *Apeomys* Fahlbusch (1968). *Arikareeomys* lacks the basic "omega" pattern of the molars typical of other eomyids. A P^4 larger than M^1 is seen elsewhere among eomyids only in *Yoderimys*. *Arikareeomys* differs from *Yoderimys* in having higher crown height and lacking P^3.

Arikareeomys skinneri, new species
(Fig. 14A, B; Table 11)

Holotype.—UNSM 81031, partial maxilla with $RP^4–M^1$.

Referred specimen.—UNSM 24153, fragmentary LP_4.

Type locality.—UNSM locality Cr-117.

Diagnosis.—Same as for genus.

Etymology.—Patronym for M. F. Skinner who discovered the Mouth of McCann Canyon locality.

Description.—Zygomatic plate tilted dorsally indicating sciuromorphy; small circular depression in maxilla just anterior to P^4; cheek teeth mesodont, higher crowned than in any other North American eomyid; P^4 slightly larger than M^1 (Table 11); anterior cingulum originating near center of protoloph and running buccally to buccal margin of tooth, widely separated from protoloph; posterior cingulum running entire width of tooth and joining both hypocone and metacone, isolating enamel lake; lingual cusps obliquely compressed; metaloph not directly connected to protoloph; mesocone large with two small spurs running anteriorly and buccally; buccal spur joining paracone; buccal cusps crescentic, not bulbous; no mesostyle.

Major cusps of M^1 (paracone, hypocone, metacone, protocone) similar in shape to those of P^4; anterior cingulum connecting to both paracone and protocone, enclosing anteroposteriorly compressed enamel lake; posterior cingulum enclosing similar lake by connecting to metacone and hypocone; mesocone connected to center of metaloph; mesocone and metaloph not connected to protoloph; narrow, deep valley separating protoloph from metaloph; no mesostyle present.

P_4 trigonid narrower than talonid; anterior margin of tooth convex; anterior cingulid joining metaconid and protoconid at lingual and buccal ends; metalophid convex posteriorly; anterior cingulid and metalophid form narrow enamel lake at center of trigonid; transverse valley separating metalophid and hypolophid; minute spur arising from hypolophid anterior to hypoconid, entering central valley.

Discussion.—Arikareeomys closely resembles the early Miocene European species *Apeomys tuerkheimae* Fahlbusch (1968). *Apeomys* develops the isolated enamel lakes on the cheek teeth as in *Arikareeomys.* The D-shaped enamel lake of the trigonid of P_4 of *A. skinneri* is otherwise known only in *Apeomys.* In the latter, however, this lake is more complicated with one or more lophules entering the trigonid from either the metalophid or anterior cingulid, and the anterior cingulid joins the protoconid buccally only in very late stages of wear. In *A. skinneri,* there is no valley separating the protoconid from the buccal end of the anterior cingulid, so fusion occurs in a much earlier stage of wear. However, many differences do exist between these two rodents. *Arikareeomys* differs from *Apeomys* in being much larger, having no mesoloph on the upper cheek teeth, having higher crowned cheek teeth, and having P^4 longer than wide. There are no European Oligocene eomyid species from which *Arikareeomys* could be directly derived (Fahlbusch, 1973, 1979). Hence, the similarities between *Arikareeomys* and *Apeomys* are considered to be due to convergence.

Among the North American eomyids, the dental pattern of *Arikareeomys* most closely approaches that of Chadronian *Yoderimys.* It resembles *Yoderimys,* and differs from all other eomyids, in having P^4 larger than M^1, and in the oblique compression of the lingual cusps on the upper molars. *Arikareeomys* lacks the P^3 that is present in all known species of *Yoderimys.* The small circular depression anterior to P^4 on the holotype of *A. skinneri* is not due to breakage or chipping of the specimen. However, there is no definite indication that a tooth ever occupied this area. This small depression is possibly the partial filling of an alveolus for dP^3 due to resorption of bone.

Among species of *Yoderimys, Arikareeomys* most closely resembles early Chadronian *Y. lustrorum* Wood (1974) from the Vieja Group, Texas. *Yoderimys lustrorum* differs from the other Chadronian species, *Y. bumpi* and *Y. stewarti* (Wood, 1955; Russell, 1972; Storer, 1978) in the following characters: 1) smaller size; 2) lack of a mesolophid on P_4; 3) anterior enamel lake on P_4; 4) anterior cingulid on P^4 does not extend lingually; 5) lack of a paracone–metacone crest on upper cheek teeth; 6) lophs not well defined, consisting of narrow ridges with little or no expansion at the cusps; 7) teeth more cuspate; and 8) connection of mesocone to protoloph very weak. All of these features, as far as known, are shared by *Arikareeomys. Yoderimys burkei* Black (1965) is so poorly known that few of these characters can be examined. However, the lophs on the only known specimen of *Y. burkei* are similar to those of *Y. bumpi.*

Yoderimys lustrorum clearly does not belong to *Arikareeomys.* There are large morphologic and temporal gaps between *Y. lustrorum* and *A. skinneri,* but there is no morphological feature of *Y. lustrorum* that would eliminate it from an ancestral position with respect to *A. skinneri.* Besides the characters listed above, *Y. lustrorum* is similar to *A. skinneri* in the weakness of the connection between the mesocone and the protoloph on the upper cheek teeth. In *A. skinneri* there is no connection, and in *Y. lustrorum* this connection is very weak (Wood, 1974: fig. 35b; Wahlert, 1978:fig. 7b).

There are no known Orellan or Whitneyan species of *Yoderimys,* nor of any other rodent that might be intermediate between *Yoderimys* and *Arikareeomys.*

Subfamily Eomyinae Depéret and Douxami, 1902

Pseudotheridomys Schlosser, 1926

Pseudotheridomys sp.

(Fig. 14C–E; Table 11)

Referred specimens.—UNSM 81032, LP_4; UNSM 81091, LP^4; UNSM 24104, RM^3.

Description.—P_4 anterior cingulid and metalophulid II run entire width of tooth, joining at protoconid and metaconid, isolating enamel lake; no mesolophid (possibly fused with metalophulid II); hypolophid and posterior cingulum running entire width of tooth and joining entoconid and hypoconid; deep, narrow valley separating hypolophid from metalophulid II; thin connection between entoconid and center of posterior cingulid, dividing posterior enamel lake into two; slight swelling at center of anterior cingulid (?anteroconid).

P^4 anterior cingulum very short, restricted to anterobuccal corner of tooth, connecting to paracone; small anterior spur on metaloph (=mesocone); posterior cingulum parallel to metaloph, not running entire length of tooth; short spur arising from paracone, directed posteriorly, not blocking central valley of tooth buccally.

M^3 protoloph straight buccolingual loph, no protoconule; protocone crescentic; anterior cingulum joining protocone and paracone at lingual and buccal ends, respectively; no mesoloph; mesocone central, joining metaloph; metaloph reduced (buccolingually); posteroloph convex posteriorly joining metaloph at both ends.

Discussion.—Two specimens of *Pseudotheridomys* cf. *P. hesperus* described by L. J. Macdonald (1972) from a Monroe Creek anthill fauna in South Dakota belong to the same species as the Nebraska specimens, based on similarity of size and direct comparison of P^4. The only difference in the morphology of the South Dakota P^4 and UNSM 81091 is the total lack of any mesocone and the isolation of the buccal anterior cingulum on the former. The latter difference is clearly due to the late stage of wear of UNSM 81091.

The upper molar from South Dakota (LACM 123525) is similar to the Nebraska M^3. It is more anteroposteriorly compressed than P^4 and wider (buccolingually). It has a distinct mesocone but no mesoloph and the anterior cingulum extends from buccal margin of the protocone to the buccal edge of the tooth. The posterior cingulum extends the entire width of the tooth.

Pseudotheridomys sp. most closely resembles the Hemingfordian *P. hesperus* from Colorado (Wilson, 1960). Both have the protoloph separated from the metaloph by a relatively deep valley with no connection by way of an anteroposteriorly directed loph, and having no, or a reduced, mesoloph on the upper cheek teeth. Fahlbusch (1968:fig. 1h) figured an isolated upper molar of *P. pusillus* from the late Oligocene of Germany that had no mesoloph and lacked a connection between the metaloph and protoloph. However, other specimens referred by Fahlbusch to this species had long mesolophs that frequently fused buccally with the paracone, as in all other species of *Pseudotheridomys* (Engesser, 1979). *Pseudotheridomys* sp. also differs from all other species of the genus by the absence of a distinguishable mesolophid on P_4. J. E. Martin (1976) reported a P_4 of *Pseudotheridomys* sp. from the younger (Hemingfordian) Batesland Formation in South Dakota that also lacked a mesolophid on P_4. The McCann Canyon specimens are larger than any other species of *Pseudotheridomys. Pseudotheridomys* sp. differs from the younger *P. hesperus* in the weak development of the anterior cingulum on P^4, having no mesoloph on the upper molars or mesolophid on P_4, and being much larger.

The morphology of the upper cheek teeth of *Pseudotheridomys* sp. is intermediate between that of the slightly older European *P. pusillus* and the younger *P. hesperus* from North America. Since the presence of a mesoloph on the upper molars of *P. pusillus* is variable, the North American species (*Pseudotheridomys* sp. and *P. hesperus*) could represent a radiation separate from the later European species which all possess a long mesoloph.

The P_4 of *Pseudotheridomys* sp. is problematical. All other species of *Pseudotheridomys* (except the specimen reported by J. E. Martin, 1976), including the very earliest, maintain a separate metalophid and mesolophid on P_4. The cusps on UNSM 81032 are more distinguishable and the tooth is much less lophate than in European late Oligocene species. It is possible that the species of *Pseudotheridomys* recognized by J. E. Martin (1976) is the same as the McCann Canyon species, but better material of both species is necessary before any decision can be made as to synonymy.

Engesser (1979) suggested that the North American species of *Pseudotheridomys* were separately derived from the European species, although he could determine no morphological differences between the two lineages. It is possible that the two earliest North American species, *Pseudotheridomys* sp. and *P. hesperus,* were derived from earlier Oligocene North American mesodont eomyids because these species share unique features of the upper cheek teeth. However, there are no known Orellan or Whitneyan mesodont eomyids from North America that lack a mesolophid on P_4 as does *Pseudotheridomys* sp. (Korth, 1980*a,* 1981). The posterior cingulid of the lower molars of *P. hesperus* (not known in *Pseudotheridomys* sp.) is long. The lower molars of the Orellan genera, *Paradjidaumo* and *Metadjidaumo,* have progressively shorter posterior cingulids on the lower molars. The teeth of these Orellan genera are already too lophate to be ancestral to the more cuspate P_4 of *Pseudotheridomys* sp.

Although *Pseudotheridomys* sp. is clearly a distinct species, no formal name will be given to it due to the incompleteness of available material.

Family Cricetidae Rochebrune, 1883
Leidymys Wood, 1936*d*
Leidymys cerasus, new species
(Fig. 16A–C; Table 12)

Holotype.—UNSM 24105, maxilla with RM^1–M^2.

Referred specimens.—UNSM 24021, maxilla with LM^2; UNSM 24022, LM_2; UNSM 24091, M^1; UNSM 24107, LM_1; UNSM 24206, RM_1; and UNSM 24108, mandible with LI_1.

Type locality.—UNSM locality Cr-125.

Diagnosis.—Intermediate-sized species of *Leidymys* (Table 12); anterocone on M^1 larger and extended farther anteriorly than in other species; cingulum present lingual to protocone on M^1; mesoloph on upper molars weak, short, and posterior to center of tooth; M_1 lacking mesolophid; I_1 with three longitudinal ridges as in *L. alicae.*

Etymology.—Latin, *cerasus,* cherry.

Description.—Larger than *L. parvus, L. alicae,* and *L. blacki,* smaller than *L. nematodon* and *L. lockingtonianus*; mandible dorsoventrally deep for cricetid; ventral edge of the masseteric fossa robust,

Table 12.—*Dental measurements of* Leidymys cerasus. *Measurements in mm.*

	M^1			M^2		
UNSM no.	a-p	tra	trp	a-p	tra	trp
24105 (type)	2.49	1.69	1.73	1.82	1.80	1.65
24091	2.53	1.59	1.64			
24021				1.89	1.73	1.55
	M_1			M_2		
	a-p	tra	trp	a-p	tra	trp
24107	1.88	1.12	1.31			
24206	1.91	0.94	1.23			
24022				1.90	1.34	1.43

ending just anterior to M_1; diastema short, shallow; mental foramen high on side of mandible posterior to middle of diastema; pronounced chin process present, running posteriorly to below mental foramen.

I_1 similar to that of *L. alicae* (Engesser, 1979:pl. 17, fig. e1) with three longitudinal ridges, one in center of anterior enamel surface, and two closely spaced ridges near lateral edge.

M^1 similar to specimens of other species of *Leidymys* (see appropriate figures in Wood, 1936*d*; Engesser, 1979; L. D. Martin, 1980); anterocone extending anteriorly, leaving broad basin between anterocone and protoloph; minute cuspule on anterolingual slope of anterocone on holotype; lingual cingulum forming shelf lingual to protocone; mesoloph very short and low, arising from endoloph posterior to center of tooth (closer to metaloph than protoloph).

M^2 with very short mesoloph, arising from endoloph as in M^1; large mesostyle on UNSM 24021, no mesostyle on holotype.

M_1 anteroconid small, triangular, lingual to center of tooth, connecting to metaconid by narrow loph; metoconid and protoconid subequal in size, connecting posteriorly by metalophulid II; anterior arm of protoconid short, terminating anteriorly in trigonid basin; ectolophid thin, buccal to center of tooth; mesoconid ovate, buccoligually compressed; hypolophid wider than metalophid; hypoconid and entoconid subequal in size; hypoconid crescentic, connecting to posterolophid; posterolophid running entire width of tooth, joining entoconid lingually; major cusps show no alternation; no mesolophid present.

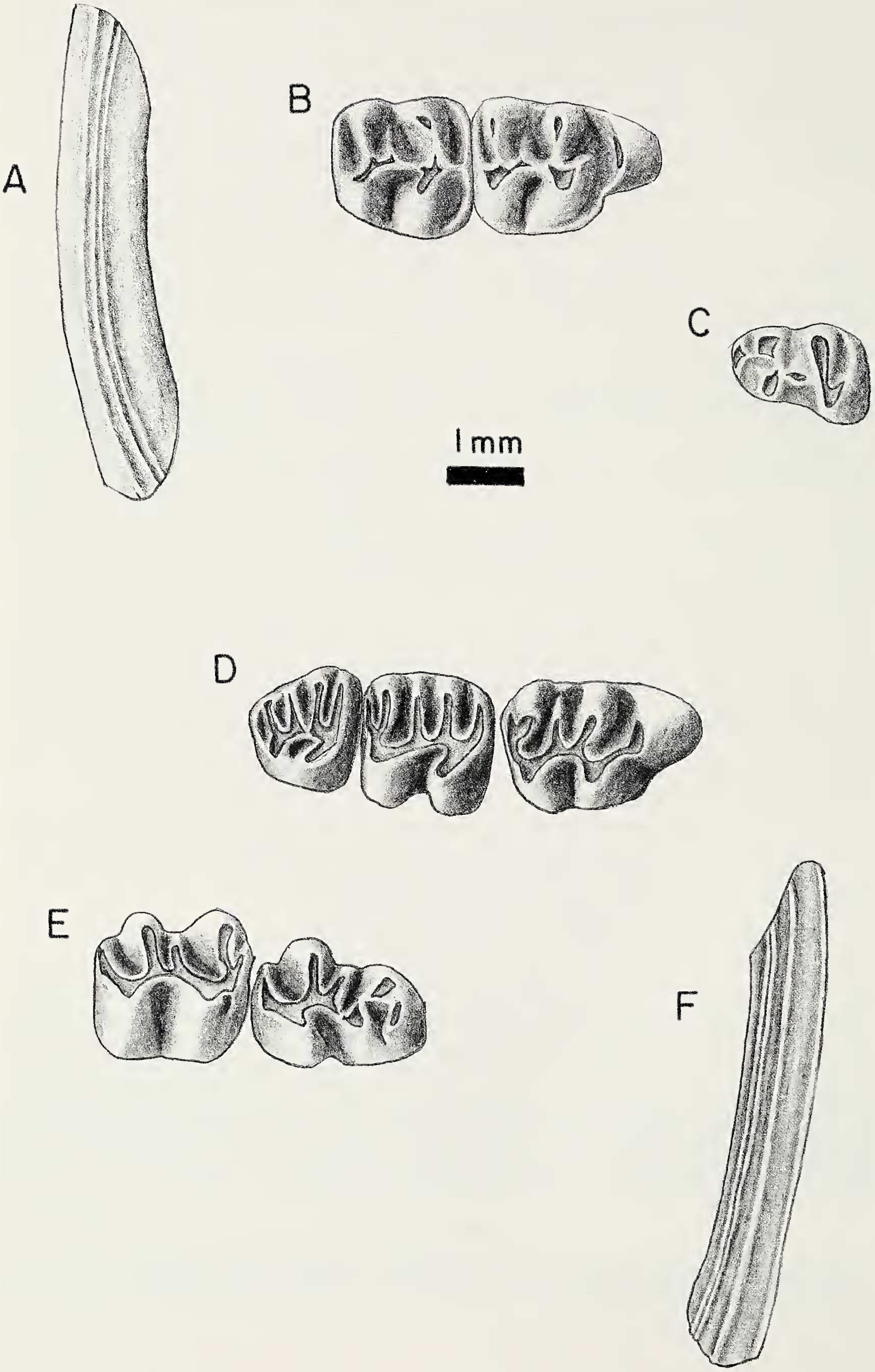
Only specimen of M_2 (UNSM 24022) heavily worn, little morphology recognizable except characteristic doubled mesolophid of *Leidymys*. Both lophids are of equal length.

Discussion.—In all dimensions of the dentition, *L. cerasus* is very near the size of specimens of *L. blacki,* the only other species of the genus from the Great Plains. The I_1 of *L. blacki* has four longitudinal ridges (L. D. Martin, 1980:fig. 26A) where *L. cerasus* has only three, as in *L. alicae.*

The anterior extension of the anterocone and the lingual cingulum on M^1 in *L. cerasus,* as well as the short, low, noncentral mesoloph of both M^1 and M^2 and lack of a mesolophid on M_1 are unique among species of *Leidymys.* All other species of the genus have long, central mesolophs on the upper molars, smaller anterocones that are more closely appressed to the protoloph on M^1, and long mesolophids on M_1. On M_2 of other species of *Leidymys,* the anterior of the two mesolophids is larger. In *L. cerasus,* the two mesolophids are short and equal in size. *Leidymys nematodon* has a shorter, noncentral mesoloph on M^2 and a more anteriorly extended anterocone on M^1. These features make *L. nematodon* closer than any other species of the genus in morphology to *L. cerasus.*

Paciculus Cope, 1879

Range.—Arikareean (late Oligocene and earliest Miocene) of Oregon, Montana, South Dakota, and Nebraska.


A
B
C
1 mm
D
E
F

Included species.—*P. insolatus* Cope, 1879 (type species); *P. montanus* Black, 1961; *P. woodi* (J. R. Macdonald, 1963); *P. nebraskensis* Alker, 1969.

Discussion.—The history of *Paciculus* is complex. Cope (1879) established the genus for the species *P. insolitus* from the Arikareean of the John Day Formation, Oregon. Later, Cope (1881*b*) referred a second John Day species, *Eumys lockingtonianus,* to the genus. Wood (1936*d*) transferred *P. lockingtonianus* to a new genus, *Leidymys,* leaving *P. insolitus* as the type and only species of *Paciculus.* Black (1961) named a new species, *P. montanus* from the Deep River Formation of Montana, which he believed to be late Hemingfordian in age. *Paciculus nebraskensis* was named by Alker (1969) from the early Arikareean Gering Formation, Nebraska. Alker also referred several other specimens from Nebraska to *Paciculus* cf. *P. insolitus.*

L. J. Macdonald (1972) cited a large sample of mainly isolated teeth from anthills in the Monroe Creek Formation, South Dakota, and referred them to *Paciculus* cf. *P. montanus.* She noted no difference in morphology between the Monroe Creek specimens and those described by Black (1961) as *P. montanus.* She failed to refer them unquestionably because the South Dakota specimens were Arikareean and those from Montana were late Hemingfordian or Barstovian. Similarly, Nichols (1976) referred several complete dentitions from an Arikareean fauna from Lemhi Valley, Idaho, to *P. insolitus,* again noting the difference in age between the Lemhi Valley specimens and those described by Black (1961).

The most recent review of the genus was by L. D. Martin (1980) who referred *Eumys woodi* Macdonald (1963) from the early Arikareean Sharps Formation, South Dakota, to *Paciculus.* Martin (1980:fig. 21a) also figured the first maxillary specimen of *P. nebraskensis,* and referred Alker's Nebraska *Paciculus* cf. *P. insolitus* to *Geringia mcgregori* (J. R. Macdonald, 1970). Martin (1980) was the first to recognize that the type material of *P. montanus* was from an Arikareean, rather than Hemingfordian, horizon (see Rensberger, 1981, for age determination).

The characters used to separate *P. insolitus* from *P. montanus* have been the proportions of the upper molars and the shape of the anterocone on M^1. In *P. insolitus* the upper molars are wider relative to length than in *P. montanus* and the anterocone on M^1 is wider (buccolingually) and does not extend as far anteriorly. The specimens identified by Nichols (1976) as *P. insolitus* have the proportions and morphology of M^1 of *P. montanus* and should be referred to that species.

L. J. Macdonald (1972:32) failed to see any difference between *P. insolitus* and *P. montanus* despite the large variation in size of the material from South Dakota and the skewed distribution of M^1 length. The isolated teeth in that sample may represent more than one taxon.

L. D. Martin (1980:fig. 20) noted that *P. nebraskensis* was smaller than *P. insolitus,* but the specimens are not figured to the same scale. The type specimens of *P. nebraskensis* and *P. insolitus* are almost exactly the same length (Wood, 1936*d*:table I; Alker, 1969:table 3). The maxillary specimen referred by L. D. Martin to *P. nebraskensis* (UNSM 11527) does not belong to this genus. It lacks

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Fig. 16.—Cricetid rodents from the Harrison Formation, Nebraska. A–C, *Leidymys cerasus.* A, UNSM 24108, LI_1 (anterior toward top of page). B, UNSM 24105 (holotype), RM^1–M^2. C, UNSM 24107, LM_1. D–F, *Paciculus nebraskensis.* D, UNSM 24110, RM^1–M^3. E, UNSM 24109, RM_1–M_2. F, UNSM 24121, RI_1 (anterior toward top of page).

Table 13.—*Dental measurements of* Paciculus nebraskensis *from Cr-117 and Cr-125. Measurements in mm.*

		N	M	OR	S	CV
M^1	a-p	24	2.45	2.17–2.71	.15	6.0
	tra	23	1.77	1.59–2.04	7.9	
	trp	23	1.73	1.52–1.96	.18	10.6
M^2	a-p	13	1.89	1.66–2.08	.10	5.1
	tra	13	1.72	1.45–1.92	.12	7.3
	trp	13	1.67	1.43–1.81	.09	5.3
M^3	a-p	4	1.46	1.41–1.54	.05	3.6
	tr	4	1.60	1.37–1.78	.15	9.3
M^1–M^3		2	5.68	5.56–5.80	—	—
M_1	a-p	16	2.28	2.07–2.55	.11	4.8
	tra	16	1.30	1.20–1.38	.05	3.9
	trp	16	1.54	1.28–1.66	.09	6.1
M_2	a-p	16	1.97	1.81–2.01	.08	3.9
	tra	15	1.62	1.42–1.73	.08	5.2
	trp	15	1.62	1.42–1.76	.08	5.1
M_3	a-p	8	1.82	1.70–1.92	.07	3.9
	tra	7	1.59	1.48–1.68	.06	4.2
	trp	7	1.28	1.10–1.43	.11	8.6
M_1–M_3		1	5.91	—	—	—

an anterocone and has a short but complex mesocone on M^1 unlike any known specimen of this genus. There is also a small spur running posterobuccally from the center of the anterior cingulum, again not known in *Paciculus.* UNSM 11527 likely represents a species of *Geringia,* or a new cricetid based on the unique morphology of the upper cheek teeth.

Paciculus nebraskensis Alker, 1969
(Fig. 16D–F; Table 13)

Referred specimens.—UNSM 24110–24116, maxillae with cheek teeth; UNSM 24109, 24120–24125, partial mandibles with cheek teeth; UNSM 24117, 24118, 24119, 24126, 24127, 24128, and 24129, isolated cheek teeth.

Emended diagnosis.—Near size of *P. insolitus* and *P. montanus,* larger than *P. woodi* (Table 13); posterior cingulum on upper molars very short; metaconid on M_1 large, connecting to protoconid; anterior cingulid separated from protoconid by deep valley on M_1; mesolophids long on molars.

Description.—Masseteric scar V-shaped, ending anteriorly below M_1; ventral ridge of masseteric scar much stronger than dorsal ridge; ascending ramus widely separated from tooth row laterally; diastema long (subequal in length to tooth row) and shallow; mental foramen at mid-depth of mandible.

I_1 flattened mesially, rounded anteriorly and laterally; enamel extending nearly half the height of the tooth on the mesial and lateral sides; four longitudinal ridges on anterior face of enamel, one along mesial corner of anterior surface, one central, and two (very closely situated to one another) lateral to center of tooth, not on lateral edge.

Cheek teeth relatively high-crowned (higher than in *Leidymys*), strongly lophate; M_1 longest lower molar; metalophid narrower than hypolophid; metaconid subequal to protoconid in size, positioned slightly anterior to protoconid; protoconid attaching to metaconid posteriorly by way of metalophulid II; anterior cingulid running buccally from metaconid, joining small anteroconid at center of tooth; buccal end of anterior cingulid free, separated from protoconid by deep valley of variable width (generally narrow); mesolophid long, extending to lingual edge of tooth; entoconid anterior to hypoconid; hypoconid crescentic; posterolophid relatively short, not extending entire width of tooth, connecting to hypoconid buccally, free lingually.

M_2 shorter and wider than M_1; metaconid even with protoconid (anteroposteriorly); anterior cingulid closely appressed to metalophid, recognizable only at buccal and lingual ends of metalophid as short spurs, disappearing completely with advanced wear; mesolophid moderate to long (not always extending to lingual edge of tooth); on UNSM 24123, mesolophid appearing as large isolated cusp; hypolophid and posterolophid as in M_1.

Metalophid and anterior cingulid of M_3 as in M_2; hypolophid narrower than metalophid, elongate posteriorly; mesolophid short, commonly uniting with entoconid lingually; hypolophid, posterolophid, and posterior cusps as in M_2 but buccolingually compressed and anteroposteriorly elongated.

Anterocone on M^1 large, buccally positioned; lingual corner of anterocone joining protoloph lingually at buccal edge of protocone; protocone and hypocone crescentic; paracone and metacone anteroposteriorly compressed; mesoloph long, reaching buccal edge of tooth; posterior cingulum very short, arising from lingual half of metaloph, extending less than half width of tooth; posterior cingulum disappearing at very early stage of wear.

M^2 nearly identical to M^1 with lack of anterocone; anterior cingulum running entire width of tooth, arising from protocone, joining paracone lingually in late wear.

M^3 smallest tooth; similar in morphology to M^2 but narrower posteriorly; protoloph and mesoloph as in M^2; metacone buccolingually compressed, joining short posteroloph posteriorly, commonly joining buccal end of mesoloph.

Discussion.—*Paciculus nebraskensis* most closely approaches *P. insolitus* and *P. woodi* in morphology. *Paciculus nebraskensis* and the latter two species differ from *P. montanus* (including "*P. insolitus*" of Nichols, 1976) in the following characters: 1) more buccal union of the anterocone to the protoloph on M^1 (with wear, this union is along the lingual margin of the tooth in *P. montanus*); 2) shorter posterior cingulum on the upper molars; 3) large metaconid united to protoconid and anteroconid on M_1 (in *P. montanus* minute to absent, not connected to protoconid, metalophulid II incomplete); 4) separation of the protoconid from buccal end of anterior cingulid (joined in *P. montanus*); and 5) anterior cingulid much more closely appressed to metalophid on M_2–M_3 (separated for almost entire width in *P. montanus*). In addition, *P. montanus* has a minute lophule running posteriorly from the center of the anterior cingulid on M_1, which is not present in *P. insolitus, P. woodi,* or *P. nebraskensis.*

Paciculus nebraskensis differs from the older *P. woodi* in being much larger (J. R. Macdonald, 1970:table 33) and having a stronger anterior cingulid on M_1. While *P. insolitus* is similar in size to *P. nebraskensis,* the width relative to the length of the upper molars of *P. insolitus* is greater than in any specimen referred here to *P. nebraskensis.*

The longitudinal ridges on I_1 of *P. nebraskensis* are similar to those figured for *P. montanus* ("*P. insolitus,*" Nichols, 1976:fig. 13A; L. D. Martin, 1980:fig. 26E). The only difference is that the two most lateral ridges are much closer together in *P. nebraskensis.*

The precise horizon of the type specimen of *P. nebraskensis* (UNSM 66166) is uncertain, but Alker (1969) and L. D. Martin (1980) suggested that it was from the early Arikareean Gering Formation, based on matrix attached to the associated postcranial elements and the identification of a specimen from the Gering referred to *P. nebraskensis.* This would make the holotype stratigraphically older than the material referred here from the McCann Canyon fauna. However, the referred specimen cited by L. D. Martin (1980) is not referable to *Paciculus* (see above discussion), and association of the postcranial elements with the dental elements of the holotype of *P. nebraskensis* is questionable. Contrary to L. D. Martin's (1980:35) discussion, fusion of the epiphyses of the questionably associated long bones of the holotype is more advanced than would be expected in an individual with the unerupted checkteeth of the holotype (L. D. Martin, 1980:fig. 22J–N). The holotype of *P. nebraskensis* much more likely came from a higher horizon than previously believed, because of the later occurrence of the Cr-117 and Cr-125 material and specimens cited by L. D. Martin (1980:35) from the Monroe Creek Formation of Wyoming.

Family Zapodidae Coues, 1875
Plesiosminthus Viret, 1926
Plesiosminthus cf. *P. clivosus* Galbreath, 1953

Referred specimen.—UNSM 24020, partial mandible with LM_3.

Locality.—UNSM locality Cr-117.

Description and discussion.—The M_3 of UNSM 24020 is heavily worn and little can be determined from the occlusal pattern of the tooth. The occlusal outline and size of the tooth are that of *Plesiosminthus.* UNSM 24020 is referred to *P. clivosus* because that is the only available name for Arikareean species of *Plesiosminthus* since Korth (1980*b*) synonymized *P. geringensis* (L. D. Martin, 1974) with the Hemingfordian *P. clivosus. Plesiosminthus clivosus* is clearly separable from *Schaubeumys* based on dental morphology (Wilson, 1960; Engesser, 1979; Korth, 1980*b*).

Order Lagomorpha Gidley, 1912
Family Ochotonidae Thomas, 1896
Gripholagomys Green, 1972
Gripholagomys lavocati Green, 1972
(Table 14)

Referred specimens.—UNSM 24159 to 24163, and 24205, isolated teeth only.

Discussion.—The UNSM specimens of *G. lavocati* do not differ in size or morphology from the slightly younger topotypic material from South Dakota. In the original description of this species, Green (1972) also referred several specimens from the Monroe Creek Formation of South Dakota. Therefore, the recognition of *G. lavocati* from the Harrison Formation does not increase the known temporal range of the species.

Family Leporidae Gray, 1821
Archaeolagus Dice, 1929
Archaeolagus cf. *A. primigenius* (Matthew, 1907)
(Table 14)

Referred specimens.—UNSM 24164, 24165, 24203, and 24204, isolated cheek teeth.

Discussion.—Reference of the Nebraska specimens to *Archaeolagus* is based on hypsodonty of the cheek teeth and the deep, straight-sided hypostriae of the isolated upper molars. The specimens from Nebraska are mostly fragmentary and there are no specimens of the diagnostic P_3, so specific identification can only be made by size. J. R. Macdonald (1970) identified a single specimen (SDSM 6294) from the Monroe Creek Formation, South Dakota as *A.* cf. *ennisianus,* a species elsewhere known from the Arikareean of the John Day Formation of Oregon (Dawson, 1958).

The measurable specimens from Nebraska are larger than *A. ennisianus* (Dawson, 1958:table 9; Table 14) but smaller than *A. macrocephalus* from the Hem-

Table 14.—*Dental measurements of lagomorphs from Cr-117 and Cr-125. Measurements in mm.*

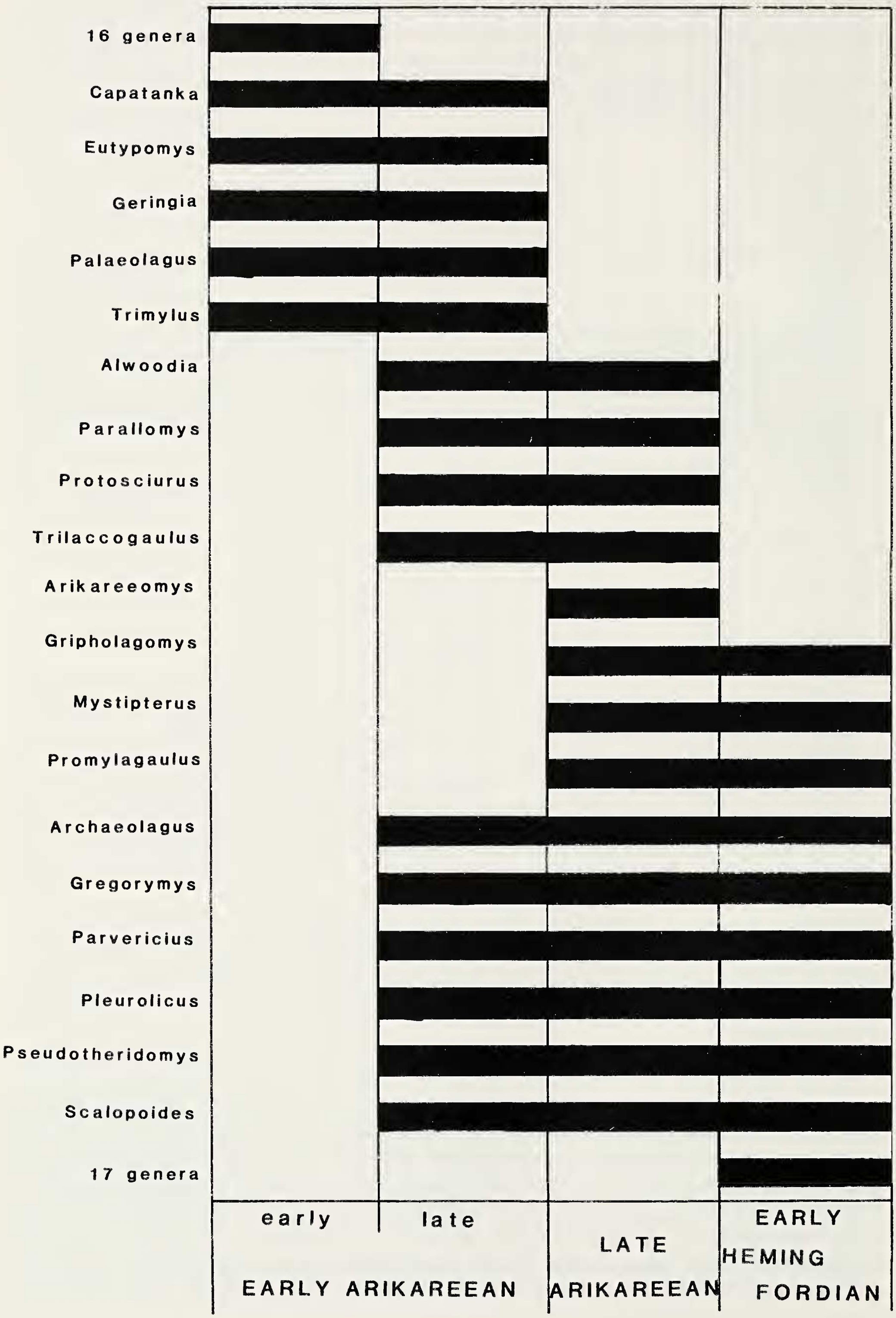
	P^2		P^3		P^4		M^1 or M^2	
UNSM no.	a-p	tr	a-p	tr	a-p	tr	a-p	tr
Archaeolagus cf. *A. primigenius*								
24203					2.51	3.88		
24164			2.15	1.97				
24164							2.15	3.74
24164							1.89	3.72
24164	1.25	2.15						
Gripholagomys lavocati								
24162	1.59	2.28						
24162			1.73	3.03				
24162			1.83	3.34				
24163			1.72	2.84				

	Lower molariform tooth			M_3		
	a-p	tra	trp	a-p	tra	trp
Archaeolagus cf. *A. primigenius*						
24204	2.76	3.12	2.29			
24164	2.45	2.30	2.02			
24164				2.32	2.24	1.74
Gripolagomys lavocati						
24159	2.09	2.36	1.66			
24159	2.03	2.47	1.72			
24159	2.07	2.28	1.57			
24159	2.07	2.20	1.50			
24159	1.93	2.25	1.69			
24159	2.06	2.12	1.50			
24159				1.71	1.62	1.14
24159				1.67	1.65	1.06
24159				1.52	1.50	1.12
24205	1.78	2.10	1.41			
24205	2.24	2.20	1.65			
24205	2.15	2.29	1.56			
24205	2.14	2.20	1.54			
24205				1.70	1.61	0.91

ingfordian Rosebud Formation. They most nearly approach the size of *A. primigenius,* which was previously known only from the same horizon (Green, 1972: table 4). Until a sample of diagnostic dentitions can be recovered, it is impossible to assign confidently the Cr-117 and Cr-125 material to any known species of *Archaeolagus.*

CONCLUSIONS

The McCann Canyon local fauna, the first diverse micromammalian fauna ever described from the Harrison Formation, can now be compared in greater detail with other Arikareean faunas, especially from the Great Plains. No rodents, lagomorphs or insectivores were used by Tedford et al. (1987) to establish the biostratigraphic boundary between early and late Arikareean, and only two rodents were used in defining the late phase of the late Arikareean (first occurrence of *Mylagaulodon* and last occurrence of entoptychine gophers). However, with the addition of the McCann Canyon fauna, the boundary between early and late


16 genera
Capatanka
Eutypomys
Geringia
Palaeolagus
Trimylus
Alwoodia
Parallomys
Protosciurus
Trilaccogaulus
Arikareeomys
Gripholagomys
Mystipterus
Promylagaulus
Archaeolagus
Gregorymys
Parvericius
Pleurolicus
Pseudotheridomys
Scalopoides
17 genera
early
late
EARLY ARIKAREEAN
LATE ARIKAREEAN
EARLY HEMINGFORDIAN

Arikareean can be better defined. The micromammalian faunas to be compared with the McCann Canyon fauna are: Sharps fauna, South Dakota (J. R. Macdonald, 1963, 1970), and Gering fauna, Nebraska (L. D. Martin, 1973)—early phase, early Arikareean; Monroe Creek fauna, South Dakota (J. R. Macdonald, 1963, 1970; L. J. Macdonald, 1972)—late phase, early Arikareean; Black Bear Quarry fauna, Rosebud Formation, South Dakota (Martin and Green, 1984), Batesland Formation fauna, South Dakota (J. E. Martin, 1976), Quarry A fauna, Colorado (Wilson, 1960), Split Rock local fauna, Wyoming (Sutton, 1972; K. Munthe, 1981; J. Munthe, 1988), Runningwater Formation faunas (L. D. Martin and Corner, 1980; Korth, et al., 1990)—early Hemingfordian. Unfortunately, no micromammalian fauna has been described from the late phase of the late Arikareean. The fauna that characterizes this phase is the Agate Springs fauna from Sioux County, Nebraska (Tedford et al., 1987), from which no small mammals have been described.

Five genera of small mammals in the early Arikareean do not survive into the McCann Canyon late Arikareean (Fig. 17): the talpid *Trimylus*; the castoroids *Capatanka* and *Eutypomys*; the cricetid *Geringia*, and the lagomorph *Palaeolagus*. Of these genera, the ranges of both *Eutypomys* and *Paleolagus* extend back into the early Oligocene, while the others first occur in the early phase of the early Arikareean. Three genera of micromammals first appear in the late Arikareean: the talpid *Mystipterus*; the rodent *Promylagaulus* and the ochotonid lagomorph *Gripholagomys*. The ranges of these genera extend into the Hemingfordian. Only one genus of rodent is restricted to the late Arikareean: the eomyid *Arikareeomys*. Five species from the McCann Canyon fauna (=late Arikareean) are advanced over known species from the early Arikareean. The insectivores *Centetodon divaricatus, Amphechinus* sp., and *Ocajila* sp. are all larger than the species of these genera from early Arikareean faunas. *Hitonkala macdonaldtau* from the McCann Canyon fauna is larger and has a more complex morphology of the upper premolar than does the early Arikareean *H. andersontau. Paciculus nebraskensis* from McCann Canyon is similarly larger with higher-crowned cheek teeth than the early Arikareean *P. woodi.*

The boundary between the early and late Arikareean as defined by Tedford et al. (1987), even with the additions cited above, is still not as distinct as boundaries between the early and late phases of the early Arikareean and the boundary between the late Arikareean and the Hemingfordian. Sixteen genera of small mammals present in the early phase of the early Arikareean are not known from any later horizon, and ten genera first occur in the late phase of the early Arikareean. Likewise, 17 genera of micromammals first appear in the Hemingfordian. Eleven genera last occur in the late Arikareean (Fig. 17). It is not known whether these genera extend into the late phase of the late Arikareean or are limited to the early phase.

The McCann Canyon fauna has greater homotaxial similarity to the Monroe Creek fauna of South Dakota than to any other fauna (Table 1). Ten species are found in common, and three are exclusive to these faunas: *Alwoodia harkseni, Parallomys americanus,* and *Trilaccogaulus ovatus.* This suggests that these faunas

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Fig. 17.—Ranges of genera of small mammals in the Arikareean and early Hemingfordian of the Great Plains.

are similar in age and that the McCann Canyon fauna is very near the early Arikareean/late Arikareean boundary.

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